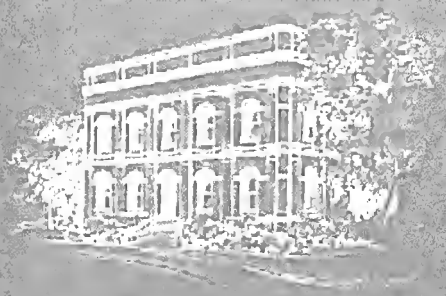
PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA



VOLUME 116 NUMBER 2 4 DECEMBER 2004
ROYAL SOCIETYS HALL 9 VICTORIA STREET MELBOURNE
VICTORIA 3000 AUSTRALIA

ESTABLISHMENT OF THE ROYAL SOCIETY OF VICTORIA

The Publications of the Royal Society of Victoria and of the Societies amalgamated with it

---

VICTORIAN INSTITUTE FOR THE ADVANCEMENT OF SCIENCE
Transactions and Proceedings, Vol 1, 1854/55.

PHILOSOPHICAL SOCIETY OF VICTORIA
Transactions, Vol. 1, 1854/55.

These two Societies then amalgamated and became—

PHILOSOPHICAL INSTITUTE OF VICTORIA
Transactions, Vol. 1-4, 1854/56-1859.

The Society then became—

ROYAL SOCIETY OF VICTORIA
Transactions and Proceedings (Vol. 5, entitled Transactions), Vol. 5-24, 1860=1887.
Transactions, Vol. 1, 2, 3 (Pt 1 only was published), 4, 5 (Pt 1 only), 6, 1888-1914.
Proceedings (New Series), Vol. 1-82, 1888-1969.
Proceedings, Vol. 83 ... 1969 ...
(*'New Series' deleted from Title Page*)

MICROSCOPICAL SOCIETY OF VICTORIA
Journal (Vol. 1, Pt 1, entitled Quarterly Journal), Vol. 1 (Pt 1 to 4), 2 (Pt 1), title page and index [all published], 1879-82.
[*The society then combined with the* ROYAL SOCIETY OF VICTORIA]
Note–Most of the volumes published before 1890 are out of print.

Vol. 46, Part 2, contains an author index of the Royal Society of Victoria and of the Societies amalgamated with it from 1855-1934.

Vol. 73 contains an author index of the Proceedings of the Royal Society of Victoria, Vol. 47 (1934/5)-70 (1958).

Vol. 84, part 2, contains an author index of the Proceedings of the Royal Society of Victoria, Vol. 71 (1959)-84 (1971).

Vol. 99, Part 4, contains an author index of the Proceedings of the Royal Society of Victoria, Vol. 85 (1972)-98 (1986).

Vol. 113, Number 1, contains an author index of the Proceedings of the Royal Society of Victoria, Vol. 99 (1987)-112 (2000).

Many of the above volumes are available for purchase. All orders should be sent to:

The Executive Officer,
Royal Society of Victoria,
9 Victoria Street,
Melbourne, Victoria 3000, Australia
Tel: (03) 9663 5259
Fax: (03) 9663 2301
Email address: rsvinc@vicnet.net.au

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

INCLUDING

TRANSACTIONS OF MEETINGS

Volume 116

NUMBER 2

MUSEUM VIC
-6 JUN 2002

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE, VICTORIA 3000

© Copyright - Royal Society of Victoria Incorporated, 2004

ISSN 0035-9211

CONTENTS OF VOLUME 116, NUMBER 2

PROCEEDINGS

M. A. Treloar & L. J. B. Laurenson
Preliminary observations on the reproduction, growth and diet of *Urolophus cruciatus* (Lacepede) and *Urolphus expansus*, McCulloch (Urolophidae) in Southeastern Australia 183

S. G. Ryan, A. D. Miller & C. M. Austin
Allozyme variation and taxonomy of the river blackfish, *Gadopsis marmoratus* Richardson, in western Victoria 191

Ilse Bartsch & Janet Gwythier
A non-indigenous halacarid species in Victoria, southeastern Australia, *Isobactrus uniscutatus* (Rhombognathinae, Halacaridae, Acari) 201

Sandford, A. C.
A revision of *Lochkovella* Chlupáč, 1972 (Arthropoda: Trilobita) and a species from Lilydale and Tyers. Phacopidae of Victoria, Part 5 207

Denis J. Carr
Lejeuneaceae (Hepaticae) of Victoria; Additions and a restitution 221

Mark Thomas Warne
Description of *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov. (Ostracoda) from the Cenozoic of S.E. Australia with comments on species of *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 from Australian and Antarctic marine waters 233

Mark Thomas Warne
Observations on *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) (Ostracoda) from the Cenozoic of S.E. Australia with comments on species attributed to *Microcytherura* Müller, 1894 and *Hemiparvocythere* Hartmann, 1982 from Australian and New Zealand marine waters 243

Patricia L. Cook & Philip E. Bock
Exechonella (Exechonellidae: Bryozoa, Cheilostomata) from the Recent and Miocene of southern Australia 251

Patricia L. Cook & Philip E. Bock
Batopora and *Lacrimula* (Batoporidae) from Australia 269

TRANSACTIONS

P.N. Joubert OAM
Some Remarks on the 1998 Sydney-Hobart Race i

Finlayson, Brian L.
The Snowy River Debate xi

EDITORIAL POLICY

The RSV disseminates new seientifie knowledge and encourages seientifie debate through the medium of its international journal *Proceedings of the Royal Society of Victoria.*

Eaeh volume of the 'Proeeedings' may eonsist of two seetions:

The 'Proeeedings' proper eonsists of peer reviewed eontributions. Each contribution is reviewed by two reviewers and. in the eases of widely divergent reviewrs opinions, a third reviewer may be consulted. The editor's deeision. through the Editorial Committee, as to the aeeeptanee or rejection of a submitted or reviewed contribution, is final.

The 'Transaetions' of the Soeiety eonsists of unreviewed items of scientifie interest sueh as oecasional addresses, artieles of debate or diseussion or other eontributions deemed appropriate by the editor and in the publie's interest. The responsibility of the content of sueh eontributions rests solely with the author.

The RSV invites eontributions for the *Proceedings* from authors across the various disciplines of the physieal and natural seienees and on issues eoneerning teehnology and the applied seienees.

Chief Editor: Montague Grover

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

PEER REVIEWED PAPERS

PRELIMINARY OBSERVATIONS ON THE REPRODUCTION, GROWTH AND DIET OF *UROLOPHUS CRUCIATUS* (LACÉPÉDE) AND *UROLOPHUS EXPANSUS*, M^{C}CULLOCH (*UROLOPHIDAE*) IN SOUTHEASTERN AUSTRALIA

M. A. Treloar & L. J. B. Laurenson

School of Ecology and Environment, Deakin University, Victoria 3280, Australia

Treloar, M. A. & Laurenson, L. J. B., 2004:12:04. Preliminary observations on the reproduction, growth and diet of *Urolophus cruciatus* (Lacépède) and *Urolophus expansus*, McCulloch (Urolophidae) in Southeastern Australia. *Proceedings of the Royal Society of Victoria* 116(2):183-190. ISSN 0035-9211.

This study examines the diet, growth and reproduction of two species of stingarees (*Urolophus cruciatus* and *U. expansus*) that occur off the south-east coast of Australia and are bycatch of commercial trawlers 5targeting latchet, flathead and jackass morwong. Both stingarees prey on similar species but in different proportions. Dominant prey for both stingarees were primarily crustaceans (isopods) followed by polychaetes. No significant difference was found between sexes though diet varied with size in both species. Sexual maturity for female and male *U. cruciatus* was attained at 320 mm and 315 mm total length, respectively. Male *U. expansus* matured at a total length of 360 mm with insufficient numbers of females to determine sexual maturity.

Keywords: Urolophids, stingarees, von Bertalanffy, prey

THE FAMILY Urolophidae (round stingrays and stingarees) contains three genera (*Urolophus, Trygonoptera* and *Plesiobatis*) and 40 species, 22 of which occur in Australian waters. Stingarees are found in habitats ranging from shallow to inner-continental waters, estuarine outlets and deep offshore waters to at least 700 meters (Last and Stevens, 1994). Two species of stingarees, *Urolophus cruciatus* and *Urolophus expansus* are commonly caught as bycatch off the southwestern coast of Victoria.

The life history of stingarees in Australia is poorly understood with only few published studies from the west coast of Australia (White, 1998; White et al., 2001) and Port Phillip Bay, Victoria (Edwards, 1980). In this paper we describe the diet, reproductive biology and age estimates of *U. cruciatus* and *U. expansus.*

MATERIALS AND METHODS

Sample collection and location

A total of 50 *U. cruciatus* and 93 *U. expansus* were collected from southwestern Victorian waters by commercial vessels targeting *Pterygotrigla polyomata* (latchet), *Neoplatycephalus auri-maculatus* (toothy flathead), *N. richardsoni* (tiger flathead) and *Nemadactylus macropterus* (jackass morwong) between March and June 2001. These specimens were bycatch of commercial otter trawls (40 m foot-line; 90 mm or 110 mm stretch mesh) fished at depths between 198 and 324 m. Trawling was conducted at speeds between 2.8 and 3 knots with sweep lengths of 180 m.

Specimens were identified and blotted dry, weighed (± 1 mm) and total length, TL (± 1 mm), disc width, DW (± 1 mm), mouth length, ML (± 1 mm) and length of tail spine (± 1 mm) recorded according to Last and Stevens (1994).

Stomachs were removed, weighed and fullness assessed using a scale from 1–5 where 1 is empty and 5 is full. Stomachs were stored in 70% ethanol and examined later under a dissecting microscope. Prey items were identified to the lowest possible taxonomic level using Jones and Morgan (1994) and Edgar (2000). Victorian Museum staff assisted when identifications could not be made from available literature. Number of prey species and the number of individual prey items were recorded for each stomach. Diet data was analysed using the Frequency of Occurrence ($F = (\frac{N}{T}) \times 100$) (Hyslop, 1980). Where N is the number of stomachs containing a particular prey item and T is the total number of stomachs examined.

Analysis of similarities (ANOSIM, PRIMER

v5.2.0) (Clarke & Gorley, 2001) was used to determine differences in diet between sex, species and size.

Reproductive development was assessed using the stages of Snelson *et al.* (1988). Female stages were; (1) immature, (2) developing, (3) mature, non-pregnant, (4) mature, pregnant, and (5) mature, post-partum. Male stages were; (1) immature, (2) maturing, virgin (3) mature, non-reproductive, and (4) mature, sexually active. Clasper length was measured to the nearest mm using callipers and clasper calcification recorded.

Vertebrae were used to obtain preliminary assessments of age. After dissection from specimens, vertebrae were immersed briefly in boiling water and cleaned of remnant connective tissue. Dried vertebrae were embedded in polyester/epoxy resin and 0.3 mm sections cut longitudinally using a diamond saw. Sections were viewed under a compound microscope

Phylum	Class/Order	Family	Species	*U. cruciatus*		*U. expansus*	
				%F	%N	%F	%N
Annelida	**Polychaeta**		**Total**	**52**	**20.37**	**26.88**	**32.95**
		Eunicidae	*Sp. 1	8	3.7	6.45	2.73
			*Sp. 2	8	1.65	8.60	1.93
			*Sp. 11	6	0.82	0	0
			*Sp. 23	0	0	3.23	0.64
		Flabelligeridae	*Sp. 10	12	4.73	2.15	4.66
		Pectinariidae	*Sp. 15	24	8.44	2.15	0.64
		Amphinomidae	*Sp. 19	0	0	12.9	22.35
		Scalibregmatidae	*Sp. 36	8	1.03	0	0
Nematoda			*Sp. 7	**10**	**1.44**	**12.9**	**3.54**
Priapulida			**Total**	**8**	**1.44**	**4.30**	**0.80**
		Priapulidae	*Sp. 16	8	1.44	2.15	0.32
			*Sp. 28	0	0	2.15	0.48
Crustacea			**Total**	**80**	**76.13**	**73**	**65.12**
	Isopoda		**Total**	**50**	**54.11**	**45.16**	**46.3**
		Cirolanidae	*Natatolana woodjonesi*	40	17.9	22.58	11.41
			Natatolana wowine	26	36.21	39.78	34.89
	Amphipoda		**Total**	**42**	**9.05**	**21.5**	**9.65**
		Phoxocephalidae	*Sp. 14	26	5.76	16.13	7.88
			Brolgus tattersalli	22	3.29	8.6	1.77
	Decapoda		**Total**	**36**	**12.97**	**31.18**	**9.17**
		Pasiphacidae	*Letochelia sydniensis*				
			(shrimp)	22	10.91	6.45	2.25
		Erangonidae	*Sp. 32 (shrimp)	12	1.85	17.2	5.47
		Palinuridae	*Jasus sp. (juvenile)*	2	0.21	0	0
		Portunidae	*Sp. 27 (crab)	0	0	2.15	0.32
		Scyllaridae	***Scyllarus crenatus***				
			(slipper lobster)	0	0	8.60	1.13
Mollusca	Cephalapoda	**Sepiolidae**	***Euprymna tasmanica***				
			(dumpling squid)	**4**	**0.41**	0	**0**
Insecta	Unknown	Unknown	*Sp. 38 (winged insect)	**1.08**	**0.16**	0	0
			*Sp. 37	0	0	**2**	**0.21**

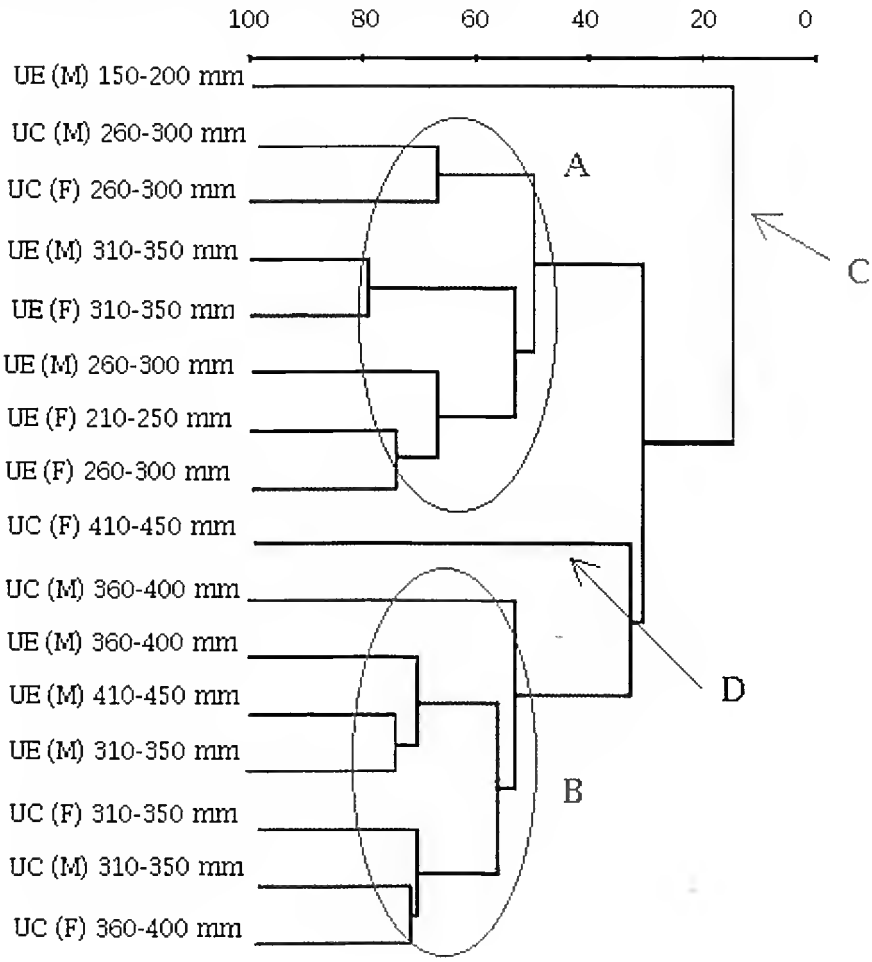
Table 1. Prey items found in Urolophus cruciatus and Urolophus expansus. Frequency of occurrence (%F) and contribution by numbers (%N) * = Unidentified.

at ∞10 magnifieation. If band definition was unelear scetions were enhanced by emersion in methyl salicylate. Band counts were repeated three times, with 25% of the samples counted by an independent reader. Growth was described using the von Bertalanffy growth model (with t constrained to 0) using Fisat II (Gayanilo and Pauly, 2001). Vertebrae were aged 'blind' and re-analysed twice for standardisation and accuraey with reader precision assessed using the Index of Average Percent Error (Beamish, 1981).

$$\text{IAPE} = \frac{100}{N}\sum_{j=1}^{N}\left(\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}\right)$$

Where
N= number of fish aged
R= the number of age determinations for each fish
X_{ij} = the *i*th determination for the *i*th fish

Fig. 1. Dendogram of variations of diet for male (M) and female (F) Urolophus expansus (UE) and Urolophus cruciatus (UC) size classes (rounded to the nearest 10 mm) caught in south-eastern Australian waters.



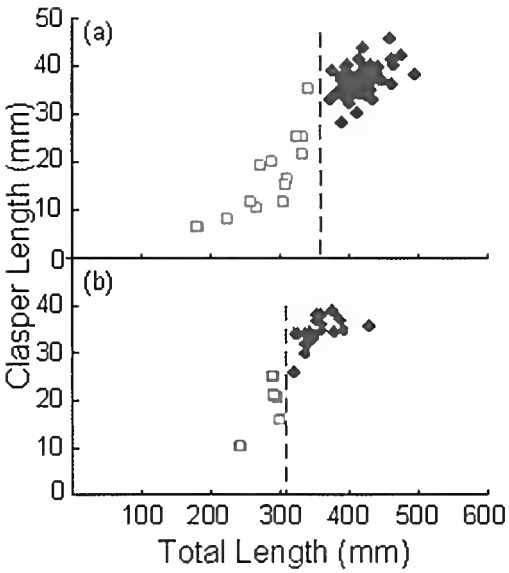


Fig 2. Relationship between clasper length (mm) and total length (mm) for male a) *Urolophus expansus* (n=79) and b) *Urolophus cruciatus* (n=27) showing onset of maturity (represented by the dashed line) by clasper calcification → and uncalcified caught from south-east Australian waters.

X_j = the average estimated age of the *j*th fish

RESULTS

Dietary composition of U. cruciatus and U. expansus

Prey species found in the stomachs of *U. cruciatus* and *U. expansus* represented six phyla and 15 families (Table 1). Crustaceans dominated the diet of both species, isopods *Natatolana woodjonesi* and *N. wowine* being the most common. Polychaetes had a higher frequency of occurrence in *U. cruciatus* while greater numbers of polychaetes occurred in the diet of *U. expansus*. Adult insects (unidentified due to being partly digested) were found in the stomachs of both species; however these results are considered an anomaly and may have been consumed by the animals while on the sorting tables of trawlers. Twenty-three prey species were present in the stomachs of both *U. cruciatus* and *U. expansus* with eleven being common to both species (Table 1).

Variations of diet between size class, sex and species

Two distinct cluster patterns and two outliers (Fig. 1) were evident in the hierarchical cluster analysis of the diet of *U. expansus* and *U. cruciatus*. The stress factor for the MDS was 0.09 suggesting a low risk of drawing false inferences (Clarke, 1993). No consistent patterns in clustering by sex or species were evident. However, distinct length-based grouping occurred with *U. expansus* differing amongst the 51–200 mm (C), 201–350 mm (A), and 351–500 mm TL (B) size classes and *U. cruciatus* differing amongst the 151–300 mm (A), 301–400 mm (B) and 401–450 mm TL (D) size classes.

Although ANOSIM demonstrated that each size class differed significantly (R=0.555), it also showed that both species were similar with an R-statistic value of 0.143 and a stronger correlation between all males and females (R= -0.012). Further analyses on male and female diet within size classes were combined because of the absence of differences in diet by sex. The R-statistic value for males and females of *U. expansus* had a close relationship of –0.031 while *U. cruciatus* followed a similar trend of R=0.019. A separate ANOSIM test on all males from both species showed a correlation between the two (R=0.105) while an individual test performed on females alone showed no similarities (R=0.648). Although there were no correlations in *U. expansus* size classes, *U. cruciatus* correlated well within its species with an R-statistic value of -0.158.

Age Estimates

A sample of 49 *U. cruciatus* and 87 *U. expansus* sections were examined under the microscope. An intra-reader precision test was performed on all readable vertebrae from both species. IAPE's for *U. cruciatus* and *U. expansus* were 7.51% and 6.02%, respectively, indicating high degrees of repeatability in the estimation of ages. Von Bertalanffy growth parameters (Table 2) showed that female *U. expansus* grow to a smaller size than males (due to absent mature female specimens the von Bertalanffy growth equation may not accurately represent growth in this species) and *U. cruciatus* females growing to a larger size than males. It should be noted that these age estimates are yet to be validated.

Reproduction

Onset of maturity for male *U. expansus* was at approximately 360 mm TL (Fig. 2a). Of the 79 male *U. expansus* examined, 16 were immature while 63 were mature. Insufficient samples of female *U. expansus* were obtained to allow assessment of onset of maturity.

Male *U. cruciatus* matured at 315 mm TL (Fig 2b). Five *U. cruciatus* males were immature while 22 were mature. Female *U. cruciatus* matured at 320 mm TL (78% of maximum observed total body length). Seven *U. cruciatus* females were immature and 16 were mature.

Male *U. expansus* and *U. cruciatus* reached sexual maturity at the age of 7 years (360 mm TL) and 6 years (315 mm TL) respectively. Female *U. cruciatus* attained sexual maturity at the age of 6 years at approximately 320 mm TL. Insufficient *U. expansus* females were collected to determine age at sexual maturity.

Macroscopic Stages of Gonads

Urolophus expansus females were either stage one or two (immature with no ovarian development or very small ovaries). No specimens larger than 350 mm TL were collected. Over 50% of female *U. cruciatus* had stage three gonads, (mature but not pregnant). Two female specimens (378 mm and 335 mm TL) possessed two pups. Male and female pups had a mean total length of 114 mm and 105 mm, respectively and mean weight of 14.5 g and 10.8 g, respectively. One female had dark trophonemata and a flaccid/enlarged uterus suggesting it had recently given birth.

Most *U. expansus* males had stage three gonads (mature but non-reproductive) or stage four gonads (mature and sexually active). Males up to 310-350 mm TL were either stage one or stage two (still maturing). *U. cruciatus* males matured earlier than *U. expansus* males as all animals were a stage three or four in the 310-350 mm TL size range.

DISCUSSION

Dietary Analysis

Urolophus cruciatus and *U. expansus* fed mostly on benthic organisms inhabiting sand and reef topography. The presence of coral, sponge and grit in their stomachs, combined with their mouth structure and morphology, suggests that these two stingarees are non-selective benthic feeders.

Crustaceans were the dominant prey in both species with isopods being the principle prey. Isopods can be parasitic or carnivorous (Hale 1927-1929) with *Natatolana* species occurring in a range of sediments into which it burrows (Johansen and Brattegard 1998), therefore it is easily preyed upon by bottom feeders. Most isopods examined were crushed and semi-digested indicating that they were presumably prey. Nematodes were found undigested in many stingaree stomachs. While there are many parasitic species in Australian temperate waters; most marine representatives live freely among the sediment and seaweed (Edgar 2000). These nematodes found were believed to be parasitic, as they were also present whole in the intestinal portion of the alimentary tract.

The presence of small numbers of benthic prey in the diet of *U. cruciatus* such as the dumpling squid

Table 2. Von Bertalanffy parameter estimates (± 1 standard error) for male and female *Urolophus cruciatus* and *Urolophus expansus* collected from south-western Victoria. Data fitted using Fisat II (Gayanilo and Pauly 2001) with t_0 constrained to 0.

Species	Sex	L_∞	k
Urolophus expansus	Female	46.95±34.6	0.21±0.44
	Male	59.56±4.29	0.14±0.03
Urolophus cruciatus	Female	50.95±4.26	0.18±0.03
	Male	46.31±4.17	0.21±0.05

(Family *Sepiolidae*) which buries itself into the sand (Norman & Reed 2000), sedentary polychaetes and amphipods suggests that *U. cruciatus* forages deeper into the sediment after prey. In contrast, *U. expansus* feeds more from the top sediments on epibenthic organisms including slipper lobsters (*Scyllarus crenatus*), crabs and more errant polychaetes that do not burrow as deeply into the sediments. ANOSIM showed extensive overlap in diet between *U. cruciatus* and *U. expansus*, despite only 11 of the 23 prey categories being common to both species.

There was no difference in diet between male and female of either species suggesting that there are no sexually based variations in foraging behaviour.

Urolophus expansus exhibited a great variation in diet with size, and fed on a range of prey species. Individuals from both species measuring between 150–300 mm TL preyed on small isopods, carid decapods and large numbers of amphipods (in different proportions). With increasing size, both species consumed a larger variety of prey with bigger isopods and amphipods ingested as well as prawns, slipper lobsters, priapulids and larger numbers of polychaetes. Isopods occurred frequently in the stomachs of all sizes of both species and the size of ingested isopods was positively correlated with stingaree size. Various studies (Andrews 1988; Kohler & Fitzgerald 1969; Platell et al. 1998) have shown that prey species are directly related to predator size. Platell et al. (1998) investigated the diet of *U. lobatus* and *U. paucimaculatus* off the south western coast of Australia in depths less than 35 m. It was found that *U. lobatus* and *U. paucimaculatus* initially fed mostly on amphipods, mysids and carid decapods. With increasing size, *U. lobatus* ingested teleosts and *U. paucimaculatus* preyed on polychaetes and penaeid decapods. Mysids were not found in the diets of *U. cruciatus* and *U. expansus*, which may be due to unavailability or selective feeding behaviours. Teleosts were not present in the diet of either species. Studies on *U. lobatus*, *U. paucimaculatus* and *Trygonoptera mucosa* in Australian waters also found that these species consumed teleosts in their adult stages (1998).

Our data suggests that *U. expansus* and *U. cruciatus* utilise similar habitats consuming 11of the same organisms but in different proportions. The reason why only 11 of the specimens preyed upon were similar could be due to their different foraging techniques and mouth structure as discussed earlier.

REPRODUCTION

Size at Sexual Maturity

Based on clasper size and calcification, male *U. expansus* and *U. cruciatus* matured at 360 mm and 315 mm TL, respectively. Last and Stevens (1994) recorded the smallest mature *U. expansus* and *U. cruciatus* males to be 410 mm and 250 mm TL, respectively. Variations with Last and Stevens (1994) may be due to different sample sizes and population differences. With a larger sample size the estimated onset of maturity may be earlier than stated.

Urolophus cruciatus females matured at 320 mm TL. Only immature female *U. expansus* were examined and so length at maturity could not be determined.

From preliminary age estimates, the youngest pregnant female and mature male *U. cruciatus* were 6+ years. The youngest mature *U. expansus* male was 7+ years.

Gestation Period

Urolophids are viviparous (trophonemata) giving birth to live young (Campbell 1996). Gestation period was difficult to determine in both species because of the lack of mature, pregnant and post-partum animals. Female pups from *U. cruciatus* measured 103 mm TL and 107 mm TL with males having a total length of 111 mm and 117 mm. The birth size is unknown for these species though it is presumed that these pups were close to being released as they were well developed. The brown stingaree (*Urolophus westraliensis*) and Coral Sea stingaree (*Urolophus* sp. B) pups are born at total lengths of 100 mm (Last & Stevens 1994). Both *U. westraliensis* and *U.* sp. B (Last & Stevens 1994) are tropical stingarees with males maturing at 240 mm and 230 mm TL respectively, a smaller size than *U. cruciatus* and *U. expansus*, suggesting a smaller length at birth.

As a generalization, stingarees have litters of two to four pups that take about three months to gestate (Last and Stevens 1994), although White et al. (2001) found that *U. lobatus* in western Australia took 10 months to gestate. Since *U. cruciatus* and *U. expansus* are also found in Australian waters gestation could also be longer than three months. If gestation is longer than three months and litters are only two to four (a low fecundity) with survival rates unknown productivity of these species could be extremely low

and commereial exploitation very dangerous.

Age and Growth

Elasmobranchs cannot at present be aged using traditional fish ageing methods, since they lack the necessary calcified structures i.e otoliths and scales. Consequently spines and vertebral centra are commonly used for age and growth studies (Callict et al. 1986; MeEachran et al. 1976). Validation was not carried out in this study due to small sample sizes. For the preliminary data required in this study it is presumed that growth bands were deposited annually, similar to other ageing studies of stingarees (White et al. 2001).

CONCLUSIONS

It was found that *U. cruciatus* and *U. expansus* are non-seleetive benthic feeders. Both speeies feed predominantly on the same organisms with isopods being the major prey item. No differences were found in the diet between males and females of the same speeies; however it was shown that diet composition and make-up varied with size. Diet variation occurred between the different size classes with smaller animals consuming smaller and fewer prey items. A greater variety of prey items became important in larger individuals.

This study has shown that *U. expansus* males mature at seven years (36 em TL, 24.7 cm DW) while female maturity could not be determined due to insufficient data. Both *U. cruciatus* sexes mature at six years though females mature at 31.5 em TL and males at 32 em TL. Dise width at maturity was 21.3 cm for both sexes.

ACKNOWLEGEMENTS

We would like to express our thanks to Deakin University for their support and the use of their facilities. The assistance of Graeme Cottier, Crisbian Ashby and fishermen for the collection of specimens were much appreciated. A big thanks to Simon Robertson from MaFRI, PhD student Sarah Irvine, Peter Last (CSIRO), William White (student from Murdoch) and to staff from Victorian Museum Martin Gomon, Gary Poore and Robin Wilson.

REFERENCES

Andrews, J. S., 1988. The feeding ecology of sand flathead (*Platycephalus bassensis*, Cuvier) from Port Phillip Bay, Victoria. *Science*. Melbourne, Victoria, La Trobe University.

Beamish, R. J., Fournier, D.A., 1981. A Method of Comparing the Precision of a set of age Determinations. *Journal of the Fisheries Research Board of Canada* 36: 735-743.

Calliet, G. M., et al., 1986. *Elasmobranch Age Determination and Verification: A Review.* Indo-Paeifie Fish Biology; Proceedings of the Second International Conferenee on Indo-Paeifie Fishes., Tokyo, Japan.

Campbell, N. A., 1996. *Biology: Fourth Edition.* The Benjamin/Cummings Publishing Company, Ine: California, America

Clarke, K.R., 1993. Non-parametrie multivariate analyses of ehanges in community structure. *Australian Journal of Ecology* 18: 117-143.

Clarke, K.R. & Gorley, R.N., 2001. Change in marine communities: an approach to statistieal analysis and interpretation. Plymouth, Primer-E Ltd.

Clarke, K.R. & Gorley, R.N., 2001. *Primer v5: User manual/tutorial.* Plymouth, Primer-E Ltd.

Edgar, G. J., 2000. *Australian Marine Life the plants and animals of temperate waters.* Sydney, Australia, Reed New Holland.

Edwards, R. R. C., 1980. Aspects of the Population Dynamics and Ecology of the White Spotted Stingarec, *Urolophus paucimaculatus* Dixon, in Port Phillip Bay, Victoria. *Aust. J. Mar. Freshwater Research* 31: 459 - 67.

Gayanilo, F. C. J. & Pauly, D., 2001. FiSAT II. Rome, Food and Agriculture Organisation of the United Nations.

Hale, H. M., 1927-1929. *The Crustaceans of South Australia*. South Australia, A. B. James Government printer.

Hyslop, E.J., 1980. Stomach Contents analysis-a review of methods and their applieation. *J. Fish. Biol* 17: 411 - 429.

Johansen, P. O. & Brattegard, T., 1998. Observations on behaviour and distribution of *Natatolana borealis*. *Sarsia* 83(4): 347-360.

Jones, D. & Morgan, G., 1994. *A Field Guide to Crustaceans of Australian Waters*, Reed Publishers.

Kohler, A.C. & Fitzgerald, D.N., 1969. Comparisons of food of cod and haddock in the Gulf of St.

Lawrence and on the Nova Scotia Banks. *Journal of Fisheries Research Board of Canada* 26: 1273-1287.

LAST, P. R. & STEVENS, J. D., 1994. *Sharks and Rays of Australia*. Hobart, CSIRO.

MCEACHRAN, J. D., et al., 1976. Food Division within Two Sympatric Species-Pairs of Skates (Pisces: Rajidae). *Marine Biology* 35: 301 - 317.

PLATELL, M. E., et al., 1998. Resource Partitioning by four species of elasmobranchs (Batoidea:Urolophidae) in coastal waters of temperate Australia. *Marine Biology* 131: 719 - 734.

SNELSON, F. F., et al., 1988. Reproduction and Ecology of the Atlantic Stingray, *Dasyatis sabina*, in Florida Coastal Lagoons. *Copeia* 3: 729 - 739.

WHITE, W. 1998. The Age Compositions, Growth Rates and Reproductive Biology of Four Species of Elasmobranchs (Batoidea: Urolophidae) in Coastal Waters of South-Western Australia, Murdoch University. THESIS

WHITE, W. T., et al., 2001. Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). *Marine Biology* 138: 135 - 147.

Manuscript received 27 July 2002
Revision accepted 4 October 2003

ALLOZYME VARIATION AND TAXONOMY OF THE RIVER BLACKFISH, *GADOPSIS MARMORATUS* RICHARDSON, IN WESTERN VICTORIA

S. G. Ryan, A. D. Miller & C. M. Austin[1]

School of Ecology and Environment, Deakin University, Warrnambool, Victoria 3280, Australia
[1] Corresponding author: (cherax@deakin.edu.au)

Ryan, S. G., Miller, A. D. & Austin, C. M., 2004:12:04. Allozyme variation and taxonomy of the river blackfish, *Gadopsis marmoratus* Richardson, in western Victoria. *Proceedings of the Royal Society of Victoria* 116(2): 191-199. ISSN 0035-9211.

A taxonomic study of the river blackfish, *Gadopsis marmoratus* was conducted using allozyme and morphological data. Focussing upon populations from western Victoria and south-eastern South Australia, a total of 147 blackfish from 14 locations were scored for variation at 28 allozyme loci. The occurrence of fixed allelic differences between samples less than 50 kilometres apart suggests that *G. marmoratus* comprises distinct northern and southern forms, consistent with previous allozyme studies. While the degree of allozyme differentiation between the northern and southern forms is small for freshwater fish species, their recognition as distinct species is justified on the basis of the limited geographic allozyme variation within each form and the finding of a geographically abrupt genetic discontinuity in western Victoria. An examination of dorsal fin spine counts also indicated differences between northern and southern forms. However, a high degree of variation within the northern form of *G. marmoratus* reduces the value of this trait for diagnostic purposes, not only for distinguishing between the two genetic forms of *G. marmoratus*, but also between *G. marmoratus* and *G. bispinosus*.

Key words: Blackfish, *Gadopsis marmoratus*, allozyme electrophoresis, morphology, taxonomy, Australia.

THE FAMILY Percichthyidae represents a distinctive element of Australia's freshwater fish fauna. Placed within this family are the morphologically distinctive gadopsid fish which are endemic to south-eastern Australia and carry out their entire life cycle in freshwater. There is conjecture on the evolutionary affinities of this taxon as it is thought that the genus *Gadopsis* has either evolved from a marine ancestor some 15 million years ago, or had a more ancient Gondwanan freshwater origin (Sanger 1984). If the latter is true the family should command a high conservation status, similar to that of the Australian lungfish (*Neoceratodus forsteri*) and the two species of Saratoga (*Scleropages* spp.) (Grant 1997).

The genus *Gadopsis* contains just two currently recognised species, *Gadopsis marmoratus* (Richardson 1848) and *G. bispinosus* (Sanger 1984). *Gadopsis marmoratus*, commonly known as the river blackfish, was described by Richardson in 1848 and was believed to be the sole gadopsid species. Some 136 years after Richardson's original description, Sanger (1984) described a second species, *Gadopsis bispinosus* the two spined blackfish, based upon morphological and allozyme data. The two species have contrasting distributions. *Gadopsis bispinosus* has a restricted distribution in the upper reaches of the Murray River, whereas *G. marmoratus* has a very wide distribution throughout the Murray-Darling River system, southern and easterly draining river systems in Victoria, and also in northerly flowing rivers of Tasmania. The species has also been introduced to southern Tasmania (Jackson et al. 1996).

The two *Gadopsis* species have been taxonomically distinguished on the basis of dorsal spine number, with *G. bispinosus* having one to three, and *G. marmoratus* having 6-13. The morphological differences between the two species are supported by allozyme data, which indicate genetic differences in sympatry (Sanger 1986).

There is, however, a degree of ambiguity regarding the taxonomy of *G. marmoratus*. McCoy (1879) described a third species, *Gadopsis gracilis* from the southern flowing Yarra River, distinguishable on the basis of head dimensions. However, Ogilby (1913) considered this to be an inconsistent trait and suggested *G. gracilis* to be a junior synonym of *G. marmoratus*. Parrish (1966) suggested *Gadopsis* from northern Tasmania to be a distinct species, however, this notion was dismissed by Sanger (1984) who considered the Tasmanian fish to be conspecific with

mainland populations. Sanger (1986) did however find allozyme variation between *G. marmoratus* populations north and south of the Great Dividing Range and he referred to these as the northern and southern forms of *G. marmoratus*.

A difficulty with the recognition of the two forms as discrete species, as pointed out by Sanger (1986), is that the degree of allozymic divergence between them is less than normally found between distinct species, and that their reproductive status cannot be determined as the two species have not been found in sympatry (Richardson et al. 1986). Sanger (1986) recommended that further taxonomic studies of the *G. marmoratus* complex be undertaken with special emphasis upon sampling in south-eastern South Australia and south-western Victoria, where he considered it likely that northern and southern forms occur sympatrically. It has also been suggested that populations of *Gadopsis* in the south-east corner of South Australia may be genetically distinct, especially those of the Ewens Ponds area, due to the species' relatively fragmented distribution in this state (Jackson et al. 1996).

The objective of this study was to extend the genetic and taxonomic research of Sanger (1986) on *G. marmoratus* via comprehensive sampling in south-western Victoria and south-eastern South Australia. The specific objectives were to: (1) determine whether sympatric populations of northern and southern *G. marmoratus* coexist in the Glenelg, Wimmera or coastal drainage's of south-western Victoria and south-eastern South Australia, as suggested by Sanger (1986); (2) evaluate the taxonomic status and genetic relationships of *G. marmoratus* samples from these regions using allozyme electrophoresis; and (3) to evaluate variation in dorsal spine counts, the principal trait used to taxonomically distinguish *Gadopsis* species.

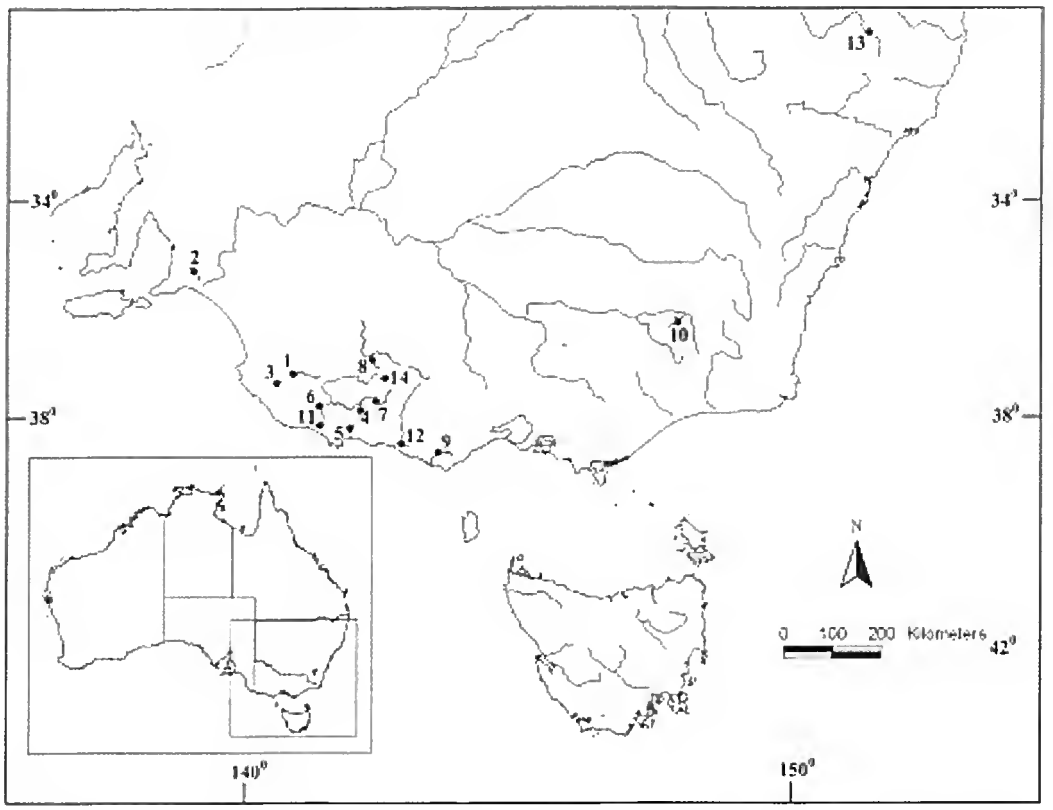


Fig. 1. Sample locations: 1. Mosquito Creek, 2. Angas River, 3. Eight Mile Creek, 4. Muddy Creek, 5. Darlot Creek, 6. Glengallan Creek, 7. Wannon River, 8. McKenzie River, 9. Gellibrand River, 10. Cudgewa Creek, 11. Glenelg River, 12. Brueknell Creek, 13. MacDonald River, 14. Scrubby Creek.

MATERIALS AND METHODS

Collection of samples

Gadopsis samples were obtained between February and September 1999 from 14 sites, three from South Australia, one from New South Wales and 10 from Victoria. Samples were collected via hook and line, bait trap, and electrofishing techniques. Four of the 14 sites were selected as reference sites based upon previous studies (Sanger 1984; Ovenden et al. 1988), including two sites from the Murray/Darling catchment for northern *G. marmoratus* (MacDonald River and Angas River), one site from a south-west Victorian coastal drainage as a reference site for southern *G. marmoratus*, (Gellibrand River), and one site in north-eastern Victoria (Cudgewa Creek) representing *G. bispinosus*.

Details of sample sites and the number of fish sampled are summarised in 'Fig. 1' and 'Table 1'. All specimens were transported back to the laboratory on ice, where they were stored at –80°C. Subsequently, liver and muscle samples were dissected from each specimen and placed into plastic vials and stored at –80°C until needed for electrophoresis. All carcasses were preserved in ethanol for later reference.

Electrophoresis

Electrophoresis was carried out using standard techniques (Farrington et al. 1999). Buffer volumes and running conditions followed standard procedures (Murphy et al. 1990) and staining solutions were prepared using standard recipes (Shaw & Prasad 1970; Harris & Hopkins 1976). All individuals were scored for variation at 28 allozyme loci. The enzyme systems used, the number of loci scored for each enzyme together with enzyme abbreviations, Enzyme Commission (EC) numbers and details of running conditions and buffers used are given in 'Table 2'. Loci were designated by abbreviations of the enzyme stains used. In the case of multiple loci for a given enzyme, they are labeled numerically starting at the locus coding for the most anodal isozyme. Cathodally migrating allozymes are designated with a minus sign. Allozymes were designated by relative mobility with the most common allozyme labelled 1.00 (Table 3).

Site	River/Creek	Species/Form[1]	Location	N
1	Mosquito Creek	*G. marmoratus* - N	S.A. (Narraeorte)	13
2	Angas River	*G. marmoratus* - N	S.A. (Strathalbyn)	4
3	Eight Mile Creek	*G. marmoratus* - N	S.A.(Ewens Ponds)	6
4	Muddy Creek	*G. marmoratus* - N	Vic (Hamilton)	15
5	Darlot Creek	*G. marmoratus* - S	Vic (Heywood)	13
6	Glengallan Creek	*G. marmoratus* - N	Vic (Dartmoor)	18
7	Wannon River	*G. marmoratus* - N	Vic (Grampians)	22
8	MeKenzie River	*G. marmoratus* - N	Vic (Wartook)	22
9	Gellibrand River	*G. marmoratus* - S	Vic (Gellibrand)	17
10	Cudgewa Creek	*G. bispinosus*	Vic (Cudgewa)	5
11	Glenelg River	*G. marmoratus* - N	Vic (Harrow)	4
12	Brueknell Creek	*G. marmoratus* - S	Vic (Brueknell)	1
13	MacDonald River	*G. marmoratus* - N	N.S.W. (Armidale)	2
14	Serubby Creek	*G. marmoratus* - N	Vic (Grampians)	5

[1] N = northern form, S = southern form

Table 1. Sample sites, including site number, abbreviated names, species or form, location of sample site and number of individuals sampled (N).

Enzyme	E. C. Number	Abbreviation	Tissue	No. of loci	Buffer system
Adenosine deaminase	3.5.4.4	ADA	L	1	TEB
Alcohol dehydrogenase	1.1.1.1	ADH	L	1	TEB
Arginine Kinase	2.7.3.3	AK	L	1	LIOH
Creatin Kinase	2.7.3.2	CK	L	1	LIOH
Esterase	3.1.1.1	EST	L	1	TEB
Fumarate Hydratase	4.2.1.2	FUMH	L	1	LIOH
General protein	———	GPT	M	3	TEB
Glycyl-L-leucine	3.4.11.	GL	L	1	TEB
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6PD	L	1	TC-6
Glutamate dehydrogenase	1.4.1.3	GDH	L	1	TEB
Glutamate-oxaloacetate transaminase	2.6.1.1	GOT	L	1	PLK
Isocitrate dehydrogenase	1.1.1.42	IDH	M	1	TEB
Lactate dehydrogenase	1.1.1.27	LDH	L	2	TEB
Malate dehydrogenase	1.1.1.37	MDH	M	1	LIOH
Malic enzyme	1.1.1.40	ME	L	1	TC-6
Mannose-6-phosphate isomerase	5.3.1.8	MPI	L	1	TC-6
Nucleoside phosphorylase	2.4.2.1	NP	L	1	TEB
L-Leucyl-glycl-glycine peptidase	3.4.11.4	LGG	L	1	TEB
L-Leucyl-proline peptidase	3.4.13.9	LP	L	1	PLK
L-Leucyl-tyrosine peptidase	3.4.13.11	LT	L	1	TEB
Phosphoglucomutase	2.7.5.1	PGM	L	1	LIOH
Phophoglucose isomerase	5.3.1.9	PGI	M	1	TEB
Sorbitol dehydrogenase	1.1.1.14	SDH	L	1	PLK
Superoxide dismutase	1.15.1.1	SOD	L	1	TEB

Table 2. Enzymes, abbreviations, Enzyme Commission (E.C.) numbers, tissue type, number of loci and buffer sustems used in the electrophoretie study of the Gadopsidae. Tissue type: L, Liver; M, Muscle. Buffer systems: TEB, Tris-EDTA-borate buffer No.6 (Selander et al. 1971); LIOH, LiOH-Boric Acid buffer No.2 (Selander et al. 1971); TC-6, Tris-citrate buffer No.4 (Selander et al. 1971); PLK, Poulik electrode buffer (Ballment et al. 1993).

Statistical analyses

Comparisons among samples were made using Nei's genetic identity, calculated from allelic frequencies, which were summarised by UPGMA clustering. All calculations were performed using the Tools for Population Genetics Analysis software package (Miller 1997).

Morphological Analysis

Variation in dorsal spine counts has been the principal diagnostic trait used to distinguish *G. marmoratus* from *G. bispinosus* (Sanger 1984). Counts were made by eye except for small specimens for which counts were determined under a dissecting microscope.

RESULTS

A total of 147 blackfish from 14 sites were scored for variation at 28 presumptive gene loci. Eighteen loci showed no variation: ADA, AK, CK, EST, FUMH, G6PD, GDH, GPT-2, GPT-3, IDH, MDH, ME, MPI, NP, LDH-2, LP, PGM, and SDH. Nine loci showed variation between sites in the form of fixed allelic differences (Table 3). Fish from Cudgewa Creek, representing *G. bispinosus*, showed the greatest divergence with fixed allelic differences at 5 of 28 loci (18 %) compared to all other samples. Fish from Darlot Creek, Brucknell Creek and the Gellibrand River were homozygous for an alternate allele at 3 out of 28 loci (equivalent to 11% fixed allelic differences) compared to all other samples excluding Cudgewa Creek (*G. bispinosus*). Fish from Darlot Creek were ho-

Locus	Allele	Site 1 Mosquito (13)	2 Angas (4)	3 Eight Mile (6)	4 Muddy (15)	6 Glengallan (18)	7 Wannon (22)	8 McKenzie (22)	11 Glenelg (4)	13 MacDonald (2)	14 Scrubby (5)	5 Darlot (13)	9 Gellibrand (17)	12 Brucknell (1)	10 Cudgewa (5)
ADH	-100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	1.00
	-25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.00
GPT-1	112	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
GL	114	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
GOT	111	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00
LDH-1	-100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	1.00
	-36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.00
LGG	106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00
	90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.00
LT	109	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
GPI	100	1.00	1.00	1.00	0.93	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00
	92	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
SOD	112	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.75	1.00	1.00	1.00	1.00	1.00

Table 3. Allele frequencies at each locus for all 14 sites of *Gadopsis* spp. Sample sizes in braekets below site codes. Loci are designated by abbreviation of the enzyme names, with multiple loci labelled numerically beginning with the locus coding for the most anodal isozyme. Cathodally migrating alleles are designated by a minus sign. Alleles are seored for relative mobility to the most common allele at each locus which is labelled 100.

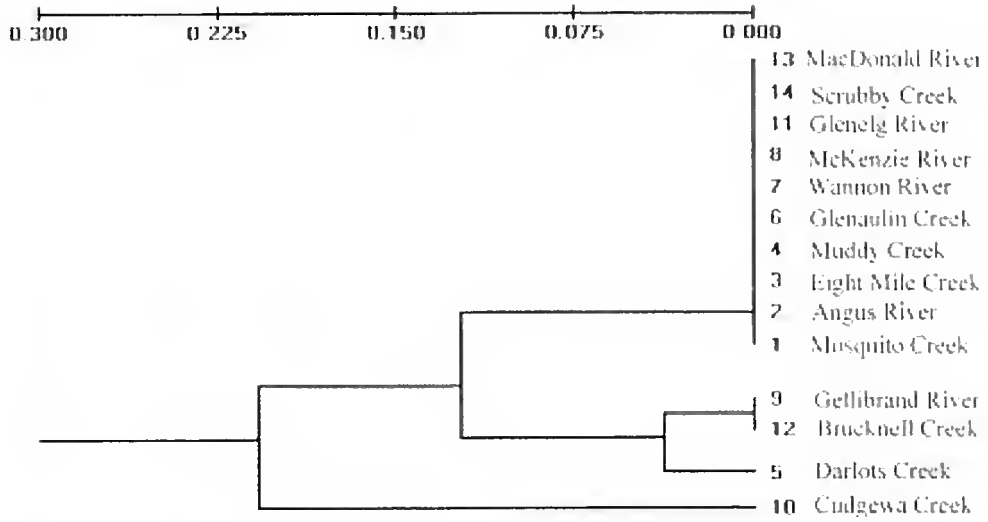


Fig. 2. UPGMA dendorgram summarizing genetic relationships among river blackfish samples derived from a matrix of Nei's unbiased (1978) Genetic Distance.

mozygous for a single unique allele at the GPI loeus. Intra-sample variation was extremely limited, consisting of a single heterozygote at eaeh of the GPI and SOD loei from the entire sample of 147 fish.

Genetic relationships among sample sites are summarised in a UPGMA dendrogram ('Fig. 2') derived from Nei's identity (1978). This analysis reveals three distinct elusters. The Mosquito, Eight Mile, Muddy, Glengallan, and Scrubby ereeks and the Angas, Wannon, MeKenzie, Glenelg, and MacDonald rivers form a single distinet group that elusters with a second comprising Darlot Creek, the Gellibrand River, and Brueknell Creek, with the most distinct sample, Cudgewa Creek, representing *G. bispinosus*. The former two elusters represent northern and southern *G. marmoratus*. Within the southern *G. marmoratus* cluster, Darlot Creek clusters apart from the other two samples on the basis of a single fixed difference at the GPI locus. Quite remarkably, with the exception of a low frequeney allele at GPI in the Muddy Creek sample, no variation was found among the samples of northern *G. marmoratus* despite these samples having been obtained from 4 major river systems (Glenelg, Wimmera, Murray and Darling rivers) and from isolated water bodies in south-eastern South Australia aeross a range of some 1,200 km.

Spine eounts could not be obtained for all fish sampled due to damage to some speeimens. 'Table 4' shows that the dorsal spine counts for *G. bispinosus* individuals was either 1 or 2, whereas the spine counts for *G. marmoratus* were highly variable, ranging from 3 to 13. Variation within samples was generally limited and conspicuous differences between populations were apparent. For example, spine counts in the Darlot Creek sample ranged from 11 to 13, whereas in the Wannon River sample they ranged from 3 to 6. The southern form of *G. marmoratus* (Brueknell Creek, Gellibrand River, Darlot Creek) had relatively high counts (9 to 13) whereas the northern form had generally lower counts (3 to 11).

DISCUSSION

Sanger (1986) reported allozyme differentiation between several populations of *G. marmoratus* from northern and southern Victoria. The results of this study extend the findings of Sanger (1986) in several respects. It has significantly increased the geographie range of sampling of *Gadopsis* for genetic and taxonomic analysis and also the number of allozyme loci examined. More specifically, it confirms that signifieant allozyme differenees occur between northern and southern forms of *G. marmoratus*. However, no evidence was found for the sympatrie oeeurrence of the northern and southern forms of blaekfish as speculated by Sanger (1986). The Fitzroy River / Darlot Creek system appears to be the most

Site	Species/Form[1]	N	Dorsal Spine Count	
			mean	range
Mosquito Creek	*G. marmoratus* - N	13	9.69	9 - 11
Angas River	*G. marmoratus* - N	4	10.50	10 - 11
Eight Mile Creek	*G. marmoratus* - N	6	9.00	8 - 10
Muddy Creek	*G. marmoratus* - N	15	8.13	7 - 9
Darlot Creek	*G. marmoratus* - S	13	12.46	11 - 13
Glengallan Creek	*G. marmoratus* - N	18	8.33	8 - 10
Wannon River	*G. marmoratus* - N	19	4.80	3 - 6
MeKenzie River	*G. marmoratus* - N	17	9.18	8 - 10
Gellibrand River	*G. marmoratus* - S	15	11.33	9 - 13
Cudgewa Creek	*G. bispinosus*	5	1.60	1 - 2
Glenelg River	*G. marmoratus* - N	4	7.75	7 - 8
Brueknell Creek	*G. marmoratus* - S	1	13.00	13
MaeDonald River	*G. marmoratus* - N	2	9.00	9
Serubby Creek	*G. marmoratus* - N	5	6.80	6 - 8

[1] N = northern form, S = southern form

Table 4. Dorsal spine counts for blackfish from 14 sites in south-eastern Australia

westerly limit of the southern form of *G. marmoratus* with the northern form appearing to be relatively common and widespread in western Victoria. In this study northern *G. marmoratus* was found at several sites in the Glenelg and Wannon river systems, the headwaters of the Wimmera River and also in the small drainages of south-eastern South Australia. The results of this study also indicate that there is no evidence for more than one taxonomic form of *Gadopsis* in South Australia (Jaekson & Llewellyn 1980).

The failure to find the northern and southern forms of *G. marmoratus* in sympatry prevents the taxonomic status of the forms from being evaluated on the basis of whether or not they are reproductively isolated. In contrast *G. bispinosus* shows five fixed differences (18.5% fixed differences) in comparison with *G. marmoratus* samples. As these genetic differences are maintained in sympatry, it can also be concluded that these taxa represent valid biological species (Sanger 1984). The determination of the taxonomic status of allopatric populations in general, and for freshwater fish in particular, is a persistent problem (McDowall 1972). However, the pattern of geographic variation in allozyme divergence within *G. marmoratus* supports the existence of two biological species.

Specifically, a striking feature of the allozyme data is the lack of genetic differentiation between samples in unconnected drainages, some 1200 km apart (ie: Wannon and MacDonald River samples). This contrasts with the four fixed allozyme differences found between populations of northern and southern *G. marmoratus* from Glengallan and Darlot Creek respectively, less than 50 km apart. These results suggest that there has been a connection between the Murray River and the rivers of south-west Victoria in the relatively recent past, and that a barrier, either biological (competitive exclusion) or geological, has existed between blackfish populations inhabiting the southerly flowing drainages in south-west Victoria for a significant period of time.

Additional support for the possibility that the northern and southern forms represent distinct species comes from an examination of evolutionary relationships of *Gadopsis* species by Ovenden et al. (1988) using restriction analysis of mitochondrial DNA. Although only based upon limited sampling of northern *G. marmoratus*, these authors found that the level of divergence between the northern and southern forms of *G. marmoratus* was of the same order of magnitude as between *G. bispinosus* and *G. marmoratus*. Further, their analyses, in contrast to the allozyme data, indicated that the relationship among the three forms were equidistant and formed an unresolved trichotomy. We are currently examining nucleotide sequence variation in the mitochondrial 12S rRNA gene region between the samples of

Gadopsis collected in this study in a effort to throw more light on the taxonomy and phylogeography of the river blackfish especially in the western parts of its distribution.

The level of intra-population variation within blackfish in this study is low and similar to the findings of Sanger (1986). The absence of allozyme variation within populations of freshwater fish species and other freshwater organisms is, however, not unusual (Campbell et al. 1994; Avery & Austin 1998; Jerry et al. 1999). The low levels of genetic diversity within populations of freshwater organisms is usually attributed to low or fluctuating population sizes and the discontinuous nature of freshwater environments. Under these circumstances genetic variation will be lost due to stochastic processes (genetic drift and founder effects) and the introduction of new genes into populations will be uncommon as gene flow will be rare between isolated water bodies.

Sanger (1986) used dorsal spine number to distinguish *G. bispinosus* and *G. marmoratus*. According to Sanger (1986), *G. bispinosus* exhibits a dorsal spine range of 1 to 3 and *G. marmoratus* a range of 6 to 13. New dorsal spine count data from this study indicates that this character is more variable than previously realised in *G. marmoratus*, with individuals from the Wannon River having counts ranging down to 3. Thus while this trait remains an important taxonomic characteristic, it cannot be considered a completely reliable diagnostic feature for distinguishing between *G. bispinosus* and *G. marmoratus*. It is also noteworthy that while northern and southern forms of *G. marmoratus* show overlap in dorsal spine counts, the northern form shows consistently lower counts compared with the southern form and therefore provides some independent support for the allozyme data.

In conclusion, although this study failed to find sympatric populations of 'northern' and 'southern' forms of *G. marmoratus*, it did discover abrupt genetic discontinuity between them in western Victoria. This supports their recognition as discrete species. We recommend that a decision on the appropriate names for the species identified in this study be held in abeyance pending a thorough taxonomic review. A major issue affecting the nomenclature of blackfish is uncertainty regarding the type locality for *G. marmoratus*, which may have been within the range of either northern or southern forms (Richardson, 1848, Ogilby, 1913).

ACKNOWLEDGEMENTS

The authors would like to thank all those who contributed to this study. Many thanks to Dr. Dean Jerry from James Cook University, Townsville, for supplying *G. bispinosus* samples, and Daniel Ierodiaconou from the School of Ecology and Environment, Deakin University, Warrnambool, for GIS support. We would also like to acknowledge Dr. Christopher P. Burridge from the Molecular Ecology and Biodiversity Laboratory, Deakin University, Warrnambool, for his contribution to the revision of this manuscript, and to the team at the Molecular Ecology and Biodiversity Laboratory for their support, especially Lachlan Farrington and Leon Meggs for their assistance in both the field and the laboratory.

REFERENCES

Avery, L. & Austin, C. M., 1998. A biochemical taxonomic study of spiny crayfish of the genera *Astacopsis* and *Eusastacus* (Decapoda: Parastacidae) in south-eastern Australia. *Memoirs of the Museum of Victoria* 56 (2): 543-555.

Ballment, E., Frusher, S. & Benzie, J. A. H., 1993. Techniques for electrophoresis of enzymes from the giant tiger prawn, *Penaeus monodon* (Crustacea : Decapoda). *A.I.M.S. Report Number 7*. Australian Institute of Marine Science, Townsville.

Campbell, N. J. H., Geddes, M. C. & Adams, M., 1994. Genetic variation in yabbies, *Cherax destructor* and *C. albidus* (Crustacea: Decapoda: Parastacidae), indicates the presence of a single, highly sub-structures species. *Australian Journal of Zoology* 42: 745-760.

Farrington, L. W., Austin, C. M., & Coutin, P. C., 1999. Allozyme variation and stock structure in the black bream, *Acanthopagrus butcheri* (Munro) (Sparidae) in southern Australia: implications for fisheries management, aquaculture and taxonomic relationship with *Acanthopagrus australis* (Gunthur). *Fisheries Management and Ecology* 7: 265-279.

Grant, E. M., 1997. *Grant's Guide to Fishes*. Grant Pty Limited. Australia, 786-789 pp.

Harris, H. & Hopkinson, D. A., 1976. *Handbook of Enzyme Electrophoresis in Human Genetics*. North Holland Publishing Company, Amster-

dam.

Jackson, P. D., Koehn, J. D., Lintermans, M. & Sanger, A.C., 1996. Freshwater Blackfishes. In *Freshwater Fishes of South-Eastern Australia*. McDowall R. M., Reed Books Australia, 186-190.

Jackson, P. D. & Llewellyn, L. C., 1980. Family Gadopsidae – River Blackfish. In *Freshwater Fishes of South-eastern Australia*. McDowall R. M., Reed Books Australia, 160-161.

Jerry, D. R., Raadik, T. A., Cairns, S. C. & Baverstock, P. R., 1999. Evidence for natural interspecific hybridization between the Australian Bass (*Macquaria novemaculata*) and estuary perch (*M. colonorum*). *Marine and Freshwater Research* 50: 661-666.

McDowall, R. M., 1972. The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxiias maculatus* (Jenyns). *Journal of the Royal Society of New Zealand* 2 (3): 325-367.

McCoy, F., 1879. Gadopsis gracilis: the Yarra blackfish. In *Prodromus of the Zoology of Victoria, Deacde III*, John Ferres, Melbourne, 39-41.

Miller, M. P., 1997. *Tools for population genetic analyses (TFPGA) 1.3*: A windows program for the analysis of allozyme and molecular population genetic data. Computer software distributed by author.

Murphy, R. W., Sites, Jr., J.W., Buth, D. G. & Haufler, C.H., 1990. Proteins: isozyme electrophoresis. In *Molecular Systematics*, Hillis, D. M. and Moritz, C. (eds), Sinauer Associates Inc., Sunderland, USA, 45-126.

Nei, M., 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583-590.

Ogilby, J. D., 1913. Edible fishes of Queesland. *Memoirs of the Queensland Museum* 2: 60-80.

Ovenden, J. R., White, R. W. G. & Sanger, A. C., 1988. Evolutionary relationships of *Gadopsis spp.* inferred from restriction enzyme analysis of their mitochondrial DNA. *Journal of Fish Biology* 32: 137-148.

Parrish, R. H., 1966. A revision of the Gadopsidae with description of a new species from Tasmania. Unpubl. MSc thesis, Oregon State University, U.S.A.. 47 pp.

Richardson, J., 1848. Ichthyology. In *The Zoology of the Voyage of H.M.S Erebus and Terror, Under the Command of Capt. Sir J. C. Ross, R.N. During the Years 1839 to 1843*. London: Longman, Brown and Longmans.

Richardson, R. J., Baverstock, P. R. & Adams, M., 1986. *Allozyme Electrophoresis*. Academic Press, Sydney, New South Wales.

Sanger, A. C., 1984. Description of a new species of *Gadopsis* (Pisces: Gadopsidae) from Victoria. *Proceedings of The Royal Society of Victoria* 96: 93-97.

Sanger, A. C., 1986. *The Evolution and Ecology of the Gadopsis marmoratus Complex*. Ph.D dissertation, University of Melbourne.

Selander, R. K., Smith, M. H., Yang, S. Y., Johnson, W. E. & Gentry, J. R., 1971. Biochemical Polymorphism and Systematics in the Genus *Peromyscus*. I. Variation in the Old-field (*Peromyscus polionotus*). In *Studies in Genetics VI*. University of Texas Publication 7103: 49-90.

Shaw, C. R. & Prasad, R., 1970. Starch gel electrophoresis of enzymes- a compilation of recipes. *Biochemical Genetics* 4: 297-320.

Manuscript received 30 March 2002
Revision accepted 21 May 2003

A NON-INDIGENOUS HALACARID SPECIES IN VICTORIA, SOUTHEASTERN AUSTRALIA, *ISOBACTRUS UNISCUTATUS* (RHOMBOGNATHINAE, HALACARIDAE, ACARI)

ILSE BARTSCH[1] & JANET GWYTHER[2]

[1]Deutsches Zentrum für Marine Biodiversitätsforschung, Forschungsinstitut Senckenberg, Notkestr. 85, 22607 Hamburg, Germany
[2]School of Ecology & Environment, Deakin University, Geelong, Victoria 3217, Australia

BARTSCH, I. & GWYTHER, J. 2004: 11: 14. A non-indigenous halacarid species in Victoria, southeastern Australia, *Isobactrus uniscutatus* (Rhombognathinae, Halacaridae, Acari). *Proceedings of the Royal Society of Victoria* 116(2): 201–206. ISSN 0035-9211.

In a temperate mangrove forest in Victoria, Australia, the mite fauna was dominated by a single halacarid species, the rhombognathine *Isobactrus uniscutatus* (Viets, 1939). The species is otherwise recorded from the northeastern Atlantic Ocean and adjacent basins. The source region of the species, Australia or Europe, and means of dispersal are discussed. *Isobactrus uniscutatus* is likely to come from northern Europe and might have been transported to Australia with hard ballast a century ago.

Key words: Marine mite, *Isobactrus*, introduced species, Australia, origin, means of dispersal

WITH world-wide travel and transport of goods, organisms are often unintentionally or intentionally introduced into new areas. One of the most important vectors is the content of ballast tanks of cargo vessels. According to recent calculations, several thousand species are transported by ship each day (Carlton & Geller 1993; Gollasch 1996). The rate of successful colonization of translocated microorganisms, plants or animals released in a new biogeographical region is unknown and many invasions might escape notice for long periods or require repeated inoculations for successful establishment. According to recent surveys of macrofauna in the ports in Victoria, shipping channels and spoil ground, about one-tenth of the marine species are non-indigenous (Cohen et al. 2001; Hewitt et al. 2004). Meiofaunal taxa such as mites are not included in these surveys.

The major marine mite family, the Halacaridae, presently includes approximately 1000 described species; beside the marine ones about 50 species are from freshwater. The mites are small-sized and exclusively benthic. Marine halacarids are present from the upper littoral to deep sea trenches, the freshwater ones from coastal zones to an altitude of 5000m. Halacarids are expected to be slow colonizers, they have no resting or planktonic stage and most species display low fecundity.

ISOBACTRUS UNISCUTATUS, A SPECIES NEW TO AUSTRALIA

Recent investigations on the meiofauna in *Avicennia* mangroves on the bank of the Barwon estuary, in the central coastal region of temperate southern Victoria, Australia, concentrated on the composition of the fauna in the mud and on the pneumatophores (Gwyther 2000). In the fouling on the pneumatophores, consisting of barnacles, algae or a combination of these epibionts, there were large numbers of marine mites, mainly halacarid mites (Halacaridae, Prostigmata) and occasionally species of gamasids (Mesostigmata) and oribatids (Ameronothroidea, Oribatida). The halacarid fauna in turn was dominated by a single species, *Isobactrus uniscutatus* (Viets 1939), a representative of the halacarid subfamily Rhombognathinae. *Rhombognathus*, another rhombognathine genus, was present though rare (Gwyther & Fairweather 2002).

SHAPE, BIOLOGY AND DISTRIBUTION OF *ISOBACTRUS UNISCUTATUS*

Isobactrus uniscutatus was first described from the Adriatic Sea of the Mediterranean (Viets 1939). Later it proved to be very abundant in the upper littoral zone in the northeastern Atlantic and North Sea (Bartsch 1972, 1976, 1978, 1979a; Green & MacQuitty 1987;

Siemer 1996). Recently the species was taken in the southwestern Pacific, in Victoria, Australia.

Adults of *I. uniscutatus* have a length of about 350–440 µm (idiosomal length), the Australian individuals have a length of 370–425 µm. The idiosoma is almost dark green, generally has a white median line and three very small red eye spots, a single anterior one near the tip of the idiosoma and a pair of lateral spots. The four pairs of legs are transparent and six-segmented; their tarsi bear smooth claws and conspicuously long and slender setae. The short gnathosoma, with its small palps and chelicerae, is largely hidden beneath the anterior end of the idiosoma. *Isobactrus uniscutatus* is algivorous, as are all other rhombognathines, and the dark green colour of the idiosoma is due to the colour of the gut with remnants of the diet showing through the transparent integument. The outlines of the long median dorsal shield (Figure 1A), the pair of short, bean-shaped ocular plates and the epimeral plates are discernible only in cleared specimens, from which the dark gut content is removed. Details of clearing halacarid mites and adequate mounting media for temporary and permanent mounts are described in Green & MacQuitty (1987).

Females and males are similar from the dorsal aspect; on the ventral side the shape of the epimeral plates is the same but the sexes differ in the genital region. The male genital opening is surrounded by a plate that bears numerous setae and two pairs of genital acetabula moved to a position posterior to the genital opening (Figure 1B). The female has three pairs of setae outside the genital plate (Figure 1C) and, as in other *Isobactrus* species, the genital acetabula are inside a cavity which is guarded by the genital sclerites.

In common with congeneric species, *I. uniscutatus* passes through four free-living juvenile instars before the adults hatch. The four instars are a larva and three nymphs, the proto-, deuto- and tritonymph. The larvae are much smaller than the adults, transparent when just hatched and, in contrast to the following instars, they bear only three pairs of legs. Aside from the smaller size, the nymphs resemble the adults; morphological differences are obvious in cleared individuals. Juveniles have no fused dorsal shield but the anterior and posterior dorsal plate separated. A genital opening is lacking, instead there is a small genital plate with one or two pairs of internal genital acetabula.

Juveniles and adults live in the same substratum wherein spermatophores and eggs are deposited. Resting, planktonic or dispersal stages are not known. Whereas most halacarids have a one-year life cycle, the genus *Isobactrus* develops quickly and can run through two generations per year (Bartsch 1972; Pugh & King 1986). The maximum number of eggs per female is 32 (Siemer 1996).

Isobactrus uniscutatus lives in and somewhat below the high water edge and is rare below the midwater line. It is a very eurytopic halacarid. In the Mediterranean, from where it was first recorded, three of the four collecting sites were strongly influenced by freshwater (Viets 1939). In the Eastern Atlantic and North Sea coast, the species is regularly taken within a salinity range from almost fresh to about 28 ‰. At about 25–28 ‰ salinity, *I. uniscutatus* is present near the high water mark, amongst lichens and films of filamentous or thin, tubular algae on stones, wooden pilings or entangled between the muddy surface of a salt marsh. The species is known to penetrate into the very diluted brackish and fresh water zone, in the river Elbe (northern Germany) into an area of less than 0.5 S‰ where typical marine algae are lacking (Bartsch 1972, 1974, 1981). Here, *I. uniscutatus* inhabits the moss *Cinclidotus* sp. The highest densities in the Weser estuary (northern Germany), with 1094 individuals per 10 cm^2, were reached in the late summer in Dedesdorf, in a predominantly oligohaline brackish-water zone (Siemer 1996). *Isobactrus uniscutatus* is found in communities not or moderately exposed to wave action but not in areas exposed to severe swell.

In the intertidal zone of the river Barwon estuary in southern Victoria, *Isobactrus uniscutatus* was abundant on fouled pneumatophores where it reached densities of 38 individuals per 10 cm^2.

As demonstrated in experiments (Siemer 1996), *I. uniscutatus* can complete a life cycle, from the egg to deposition of eggs of the raised female, within 89 days. At summer temperature (20°C) development is quickest at 15 S‰. At lower temperature the development is retarded, at 5°C it is almost stopped. When kept at salinity of 1 or 30 ‰, the time of development is 1.5 times longer than that at 15 ‰ (Siemer 1996). The dense population of *I. uniscutatus* in the freshwater zone of the river Elbe near Hamburg inplies that the species can thrive and reproduce at less than 0.5 S‰.

Short-time exposure to environmental challenges, far beyond the given limits necessary for development and reproduction, are tolerated without any obvious damage. Salinity beyond 50 ‰ is survived in an inactive state for several days; the individuals quickly recover when returned into their habitat salinity (Bartsch 1974). *Isobactrus uniscutatus* also proved to be resistant to high temperatures (Bartsch 1974). A temperature of about 39–40°C is normally not reached at the German coast, even on a very sunny summer day after hours of intense sun radiation on a quickly drying substratum. Individuals of *I. uniscutatus*

exposed to such temperatures quickly turn into an inactive state and survive (Bartsch 1974). Freezing is tolerated as well.

Though being an aquatic organism, *I. uniscutatus* can survive long-term desiccation. In experiments of 12 days exposure to air, without wetting by splash, 40 % of the animals in a test recovered (Bartsch 1974).

Siemer (1996) demonstrated that *I. uniscutatus* can be raised on a diet of *Blidingia*, a tubulose green algae often dominant in the upper littoral in marine and brackish water. The diet in the field is certainly not restricted to a single algal species but is diverse and, in adaptation to the relevant habitat, includes several food items. Beside algae, fungi or even carcasses may attract and be used by the mite.

ECOLOGY OF *ISOBACTRUS UNISCUTATUS* IN THE RIVER BARWON ESTUARY

The Barwon estuary is in the temperate southern Victorian coast of Australia (38°17'S, 144°30'E). The tidal amplitude is 1.8 m. In the upper tidal area, the mudflats are covered with mangroves, with a single tree species, *Avicennia marina* (Forsskål) Vierhapper, 1907, whose pneumatophores extend almost 20 m seaward (Gwyther 2000). The generally dense coverage by epibionts consists of algae, barnacles or a mixture of both. On algal fouled pneumatophores marine mites represented 31% of the epiphytic meiofauna (Gwyther 2000), with *I. uniscutatus* being the numerically most important taxon. On pneumatophores fouled with

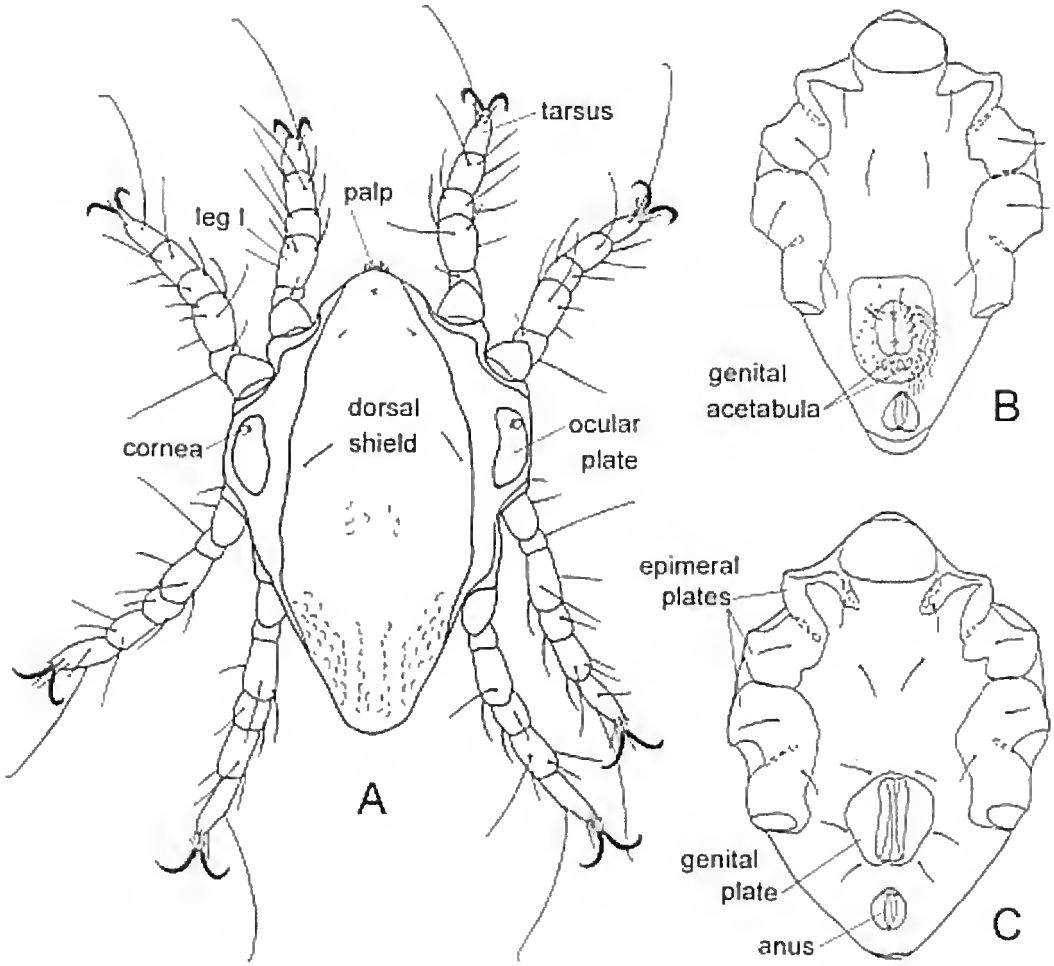


Fig. 1. *Isobactrus uniscutatus*, A, dorsal aspect; B, idiosoma, ventral aspect, male; C, idiosoma, ventral aspect, female.

barnacles, this single mite species comprised almost 91% of the epibiotic meiofauna. It reached densities of 500–1000 individuals per pneumatophore. Marine mites were rare in the muddy sediment and amongst the leaf litter of the forest floor.

THE GENUS *ISOBACTRUS*

At present, the genus *Isobactrus* contains 26 species. All records of *Isobactrus* are from near the water edge, the majority from areas regularly or irregularly emerged, from coastlines under tidal influence or basins with irregular oscillations. The genus is spread worldwide, present in almost all latitudes, from 75°N, on the coasts of Nowaja Semlja in the North Polar Sea, over warm and tropical shores (Galapagos Island, Micronesia) to the cold-temperate and sub-Antaretic (South America, South Georgia, Prince Edward Island, Kerguelen, Macquarie Island) (Bartsch 2003c).

More species of *Isobactrus* are recorded from the northern than from the southern hemisphere (Bartsch 2003c). In the North Atlantic and adjacent basins, *Isobactrus* often is present in high densities, whereas in tropical and southern hemisphere regions, *Isobactrus* seems to be rare. Three species have been previously recorded from Australia, *I. ponapensis* Abé, 1996 from the Great Barrier Reef, *I. australiensis* Bartsch, 2003 and *I. obesus* Bartsch, 1992 from tropical Western Australia (Bartsch 2000, 2003a). *Isobactrus uniscutatus* is the fourth *Isobactrus* species from Australia and the first from Victoria, and, in contrast to the other species, it lives in dense populations.

GEOGRAPHIC ORIGIN OF *ISOBACTRUS UNISCUTATUS* AND MEANS OF DISPERSAL

Isobactrus uniscutatus is believed to be no native Australian species but to have been transported from Europe to Australia; here it found a suitable habitat to colonize. The extent of its present distrihution along the Victorian coastline is unknown.

The genus *Isobactrus* inhabits latitudes from 75°N to 55°S, but there are clear differences between species from the northern and southern hemisphere (Bartsch 2000, 2003c; Abé 2001). In species from the northern Atlantic and Pacific the anterior epimeral plates are small, the dorsal setae on the idiosoma are slender, and in a few species the number of setae is less than the five pairs present in the majority of all halacarids. Species from the warm-temperate and tropical Indo-West Pacific and the southern hemisphere have larger anterior epimeral plates, the species have five pairs of dorsal setae on the idiosoma but the setae are short and spur-like. Compared to congeners from the north, often the numbers of setae on the third and fourth leg segments are reduced. The species from cold-temperate and sub-Antaretic areas differ from species from the tropics by the large anterior epimeral plates being fused in the median and the presence of a dorsolateral seta on the third epimeral plate.

Abé (2001), after a phylogenetic analysis based on morphological characters, distinguished between three major groups which in turn proved to be bound to geographic regions. One group includes species of the northern seas, the Northern Pacific, Northern Atlantic and adjacent basins, another is restricted to the tropical/warm-temperate Indo-West Pacific region; these species in turn are distinct from those recorded from the cold southern hemisphere shores.

Isobactrus uniscutatus is a typical northern Atlantic species and, moreover, it shares several characters with *I. hutchinsoni* Newell, 1947, an eastern North American species (Newell 1947), characters not found in any of the other *Isobactrus* species (Bartsch 1979b, 2003c). We suggest that the presence of *I. uniscutatus* in Victoria most certainly is the result of human activity, and it is unlikely that it is a relict of a former fauna. This raises the questions of how and when this species arrived in Australia.

Mechanisms of transfer to foreign coastlines, for example to the Mediterranean and North America are summarized in Zibrowius (1991) and Ruiz et al. (1997). Vectors which can be excluded with respect to *I. uniscutatus* are: (1) transport by aquarium equipment: such a transport is thought to be responsible for long-distance spreading of the algae *Caulerpa taxiflora* (M. Vahl) C. Agardh, 1817 (Withgott 2002); (2) transport by marine packing material: organic packing material (algae) is used over short distances but certainly not in intercontinental journeys; (3) transport together with intentionally introduced species and equipment, e.g. together with organisms for aquaculture. Cultures from offshore areas are not expected be contaminated by *I. uniscutatus*, but there is a small chance that equipment in semi-enclosed bays or nearshore brackish-water areas is colonized by this halacarid and then transported.

The most important vector in unintentional translocation of marine organisms is transport by ship, either on the hull or with the contents in ballast tanks. In the case of *I. uniscutatus*, a recent transportation on the hull of a ship can be rejected because the halacarid fauna in harbours nowadays generally is poor (most likely due to frequent destruction of the habitat by

abrasion, oil spill and other chemical pollutants) and even if some halacarid specimens should be able to settle amongst the fouling, they would be washed off during the passage from Europe to Australia. Transport in ballast water is unlikely, too, as halacarids have no planktonic stages. The number of species washed out from their habitats seems to be negligible, and, as mentioned above, the halacarid fauna in harbours is sparse. The mite mentioned by Carlton & Geller (1993) from ballast water is expected not to be a halacarid mite but one of the semiterrestrial or terrestrial living forms which now and then are found drifting near the shoreline (e.g. the mite mentioned by Armonies 1989).

Still, *I. uniscutatus* is likely to have been transported by ship. Prior to the middle of the 19th century, sand and boulders were used as ballast (Carlton 1985). Algae-covered stones and boulders from the shoreline, often stored in special areas, provided an ideal substratum for benthic meiofaunal organisms. As shown above, *I. uniscutatus* is at least in experiments resistant to a deteriorating environment, and a part of a founder population, with both female and male individuals, should have been able to survive transport by ship, wetted by splash now and then. As *I. uniscutatus* can live in a wide range of substrata, salinity, temperature, tidal emergence, and feed on different food items, it is likely that it found an unoccupied niche in a brackish-water environment. With its rather high rate of development, approximately 20 eggs per female and two or three generations a year, this halacarid species had a good chance to establish itself successfully in Australia.

DISTRIBUTION IN AUSTRALIA

At present, records of *Isobactrus uniscutatus* are restricted to the river Barwon estuary, Victoria. The mite is numerous amongst pneumatophores of the mangrove *Avicennia marina*. The extent of the geographic distribution westwards towards Spencer Gulf, or eastwards to the coast of New South Wales is not known. The species obviously has not reached Perth, Western Australia. During a short stay-over in the austral winter 2000, the first author (I.B.) examined the banks of the Swan River, expecting to find halacarid species adapted to the fluctuating salinity in the Swan river. The only mite species regularly present in the samples of algae and deposits between roots of *Juncus* was a representative of the halacarid genus *Copidognathus* (Bartsch 2003b). No *Isobactrus* species was collected. Should *I. uniscutatus* be transported into the mouth of the Swan river, it is likely to be able to become established as the mite fauna in the Swan river proved to be sparse and *I. uniscutatus* would not have to compete with any native halacarid species.

REFERENCES

Abé, H., 2001. Phylogeny and character evolution of the marine mite genus *Isabactrus* (Acari : Halacaridae). *Journal of Natural History* 35: 617–625.

Armonies, W., 1989. Occurence of meiofauna in *Phaeocystis* foam. *Marine Ecology Progress Series* 53: 305–309.

Bartsch, I., 1972. Ein Beitrag zur Systematik, Biologie und Ökologie der Halacariden (Acari) aus dem Litoral der Nord- und Ostsee. I. Systematik und Biologie. *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins zu Hamburg (Neue Folge)* 16: 155–230.

Bartsch, I., 1974. Ein Beitrag zur Systematik, Biologie und Ökologie der Halacariden (Acari) aus dem Litoral der Nord- und Ostsee. II. Ökologische Analyse der Halacaridenfauna. *Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins zu Hamburg (Neue Folge)* 17: 9–53.

Bartsch, I., 1976. Ergänzungen zur Halacariden-Fauna (Halacaridae, Acari) im Becken von Arcachon. *Vie et Milieu, série A* 26: 31–46.

Bartsch, I., 1978. Verbreitung der Halacaridae (Acari) im Gezeitenbereich der Bretagne-Küste, eine ökologische Analyse. I. Verbreitung der Halacariden. *Cahiers de Biologie Marine* 19: 363–383.

Bartsch, I., 1979a. Verbreitung der Halacaridae (Acari) im Gezeitenbereich der Bretagne-Küste, eine ökologische Analyse. II. Quantitative Untersuchungen und Faunenanalyse. *Cahiers de Biologie Marine* 20: 1–28.

Bartsch, I., 1979b. Halacaridae (Acari) von der Atlantikküste Nordamerikas. Beschreibung der Arten. *Mikrofauna des Meeresbodens* 79: 62 pp.

Bartsch, I., 1981. Meeresmilben der Umgebung von Hamburg (Arach.: Acari: Halacaridae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (Neue Folge)* 24: 5–18.

Bartsch, I., 2000. Rhombognathinae (Acari: Halacaridae) from the Great Barrier Reef, Australia. *Memoirs of the Queensland Museum* 45: 165–203.

Bartsch, I., 2003a. Mangrove halacarid fauna

(Halacaridae, Acari) of the Dampier region, Western Australia, with description of five new species. *Journal of Natural History* 37: 1855–1877

Bartsch, I., 2003b. A new species of *Copidognathus* (Acari: Halacaridae: Copidognathinae) from Western Australia , with notes on Halacaridae in fresh and brackish water. In *An Acarological Tribute to David R. Cook - From Yankee Springs to Wheeny Creek*. I. Smith, ed, Indira Publishing House, West Blomfield, Michigan, 11–19.

Bartsch, I., 2003c. The subfamily Rhombognathinae: developmental pattern and re-evaluation of the phylogeny (Arachnida, Acari, Halacaridae). *Senckenbergiana biologica* 82: 15–57.

Carlton, J. T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanography and Marine Biology, Annual Review* 23: 313–371.

Carlton, J. T. & Geller, J. B., 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261: 78–82.

Cohen, B. F., McArthur, M. A. & Parry, G. D., 2001. Exotic marine pests in the Port of Melbourne, Victoria. *Marine and Freshwater Resources Institute Report* 25: 96 pp.

Gollasch, S., 1996. *Untersuchungen des Arteintrages durch internationalen Schiffsverkehr unter besonderer Berücksichtigung nichtheimischer Arten*, Kovac, Hamburg, 210 pp.

Green, J. & MacQuitty, M., 1987. Halacarid Mites. *Synopses of the British Fauna, New Series* 36: 178 pp.

Gwyther, J., 2000. Meiofauna in phytal-based and sedimentary habitats of a temperate mangrove ecosystem – a preliminary survey. *Proceedings of the Royal Society of Victoria* 112: 137–151.

Gwyther, J. & Fairweather, P.G., 2002. Colonisation by epibionts and meiofauna of real and mimic pneumatophores in a cool temperate mangrove habitat. *Marine Ecology Progress Series* 229: 137–149.

Hewitt, C. L., Campbell, M. L., Thresher, R. E., Martin, R. B., Boyd, S., Cohen, B. F., Currie, D. R., Gomon, M. F., Keough, M. J., Lewis, J. A., Lockett, M. M., Mays, N., McArthur, M. A., O'Hara, T. D., Poore, G. C. B., Ross, D. J., Storey, M. J., Watson, J. E. & Wilson, R. S. 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Marine Biology* 144: 183–202.

Newell, I.M. 1947. A systematic and ecological study of the Halacaridae of eastern North America. *Bulletin of the Bingham Oceanographic Collection* 10: 1–232.

Pugh, P. J. A. & King, P. E., 1986. Seasonality in some British intertidal Acari. *Journal of Natural History* 20: 653–666.

Ruiz, G. M., Carlton, J. T., Grosholz, E. D. & Hines, A. H., 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37: 621–632.

Siemer, F., 1996. *Untersuchungen zur Verteilung, zur Biologie und zum Lebenszyklus mariner Halacaridae (Prostigmata: Acari) im ästuarinen Felslitoral*, Ph. D. thesis, University of Bremen, 165 pp.

Viets, K., 1939. Meeresmilben aus der Adria (Halacaridae und Hydrachnellae, Acari). *Archiv für Naturgeschichte (Neue Folge)* 8: 518–550.

Withgott, J., 2002. California tries to rub out the monster of the Lagoon. *Science* 295: 2201–2202.

Zibrowius, H., 1991. Ongoing modification of the Mediterranean marine fauna. *Mésogée* 51: 83–107.

Manuscript received 15 September 2002
Revision accepted 10 July 2003

A REVISION OF *LOCHKOVELLA* CHLUPÁC, 1972 (ARTHROPODA: TRILOBITA) AND A SPECIES FROM LILYDALE AND TYERS. PHACOPIDAE OF VICTORIA, PART 5.

A. C. SANDFORD

School of Earth Sciences, University of Melbourne, Victoria, 3010, Australia. E-mail address: andrewsandford@hotmail.com

SANDFORD, A. C., 2004:12:04. A revision of *Lochkovella* Chlupác, 1972 (Arthropoda: Trilobita) and a species from Lilydale and Tyers. Phacopidae of Victoria, Part 5. *Proceedings of the Royal Society of Victoria* 116(2): 207-220. ISSN 0035-9211.

The trilobite *Acaste longisulcatus* Shergold, 1968 was described from the Early Devonian Humevale Siltstone at Lilydale, Victoria. However the holotype, an internal mould of a pygidium, is recognised as belonging to a phacopid rather than an acastid trilobite. As the original description was largely based on the paratypes, since redescribed as *A. lokii* Edgecombe, 1993, the holotype and its species have been poorly understood. The species is assigned here to *Lochkovella* Chlupác, 1972, not previously recorded in Australia but well represented by *L. longisulcata* and three other species from Victoria and New South Wales. The relationships of *Lochkovella* are reviewed, and a revised generic diagnosis is provided. *Lochkovella longisulcata* is abundant in the middle horizons of the Humevale Siltstone at Lilydale and in the upper horizons of the Boola Formation at Coopers Creek and Tyers. The stratigraphic ranges of *L. longisulcata* and 15 other trilobite and brachiopod taxa common to the Tyers and Lilydale sequences suggest correlation of the fauna from the upper horizons of the Boola Formation with faunas from the 1 700 m – 2 400 m interval of the Humevale Siltstone at Lilydale. Age estimates on these sequences are not well constrained and range within the early Lochkovian to earliest Pragian interval, accommodating divergent interpretations of the upper boundary of the Boola Formation with the overlying Coopers Creek Limestone.

Keywords: Trilobites, Phacopidae, Systematics, Victoria, Devonian

TRILOBITES occur in abundance in the marine fauna of the Late Silurian-Early Devonian Humevale Siltstone (3 800 m thick) at Lilydale, 35 km E of Melbourne (Fig. 1). Twenty-nine trilobite species, mostly undescribed, are represented by 750 specimens from about 50 different localities between Christmas Hills (35 km ENE of Melbourne) and Lilydale, ranging variously throughout the unit (Fig. 2). A poorly documented phacopid, assigned below to *Lochkovella* Chlupác, 1972, occurs at localities at horizons between 465m and 2 400 m above the base of the unit. Occurrences of the species include locality PL1820 (G20 *'Ruddocks Quarry'*), Chirnside Park (600 m horizon) and locality PL1804 (G4, *'Flowerfield Quarry'*), Coldstream (1755 m horizon). Specimens from the latter locality were figured by McCoy (1876) as '*Phacops (Portlockia) fecundus* Barrande, 1846'. The former locality is the type locality for several trilobite species including '*Goldius' greenii* Chapman, 1915, *Sthenarocalymene angustior* (Chapman, 1915), *Acastella frontosa* Shergold, 1968 and the problematic *Acaste longisulcatus* Shergold, 1968. The latter species is not an acastid; Holloway & Neil (1982) noted that the pygidium figured by Chapman (1915) as '*Phacops crossleii* Etheridge & Mitchell, 1896' and later designated holotype of *A. longisulcatus* is a phacopid. The paratypes of *A. longisulcatus* (from PL1850 [G50, *'Black Springs Quarry'*], Chirnside Park) are not conspecific with the holotype; they belong to an acastid trilobite and were described as *Acaste lokii* Edgecombe, 1993. As the specimens of *Lochkovella* from PL1820, from PL1804 (including some of McCoy's figured specimens) and other localities are conspecific with the holotype of *longisulcatus*, they permit the redescription of *L. longisulcatus*.

Philip (1962) described a trilobite fauna from the Boola Formation at Tyers, about 130 km ESE of Melbourne, including *Cheirurus (Cheirurus)* sp. occurring at the stratigraphically lowest trilobite locality, with *C. (Crotalocephalus) silverdalensis* Etheridge & Mitchell, 1917, *S. angustior* and *Lconaspis bispinosa* Philip, 1962 occurring in the upper horizons of the unit. Philip did not record any phacopid trilobites in the Tyers fauna, but in his and other fossil collections from the area two species are represented, *Boeckops* sp. and *Lochkovella longisulcata*, the latter also occurring in the unit at Coopers Creek, about 20 km NNE of Tyers. Other trilobites occurring in the Boola Formation at

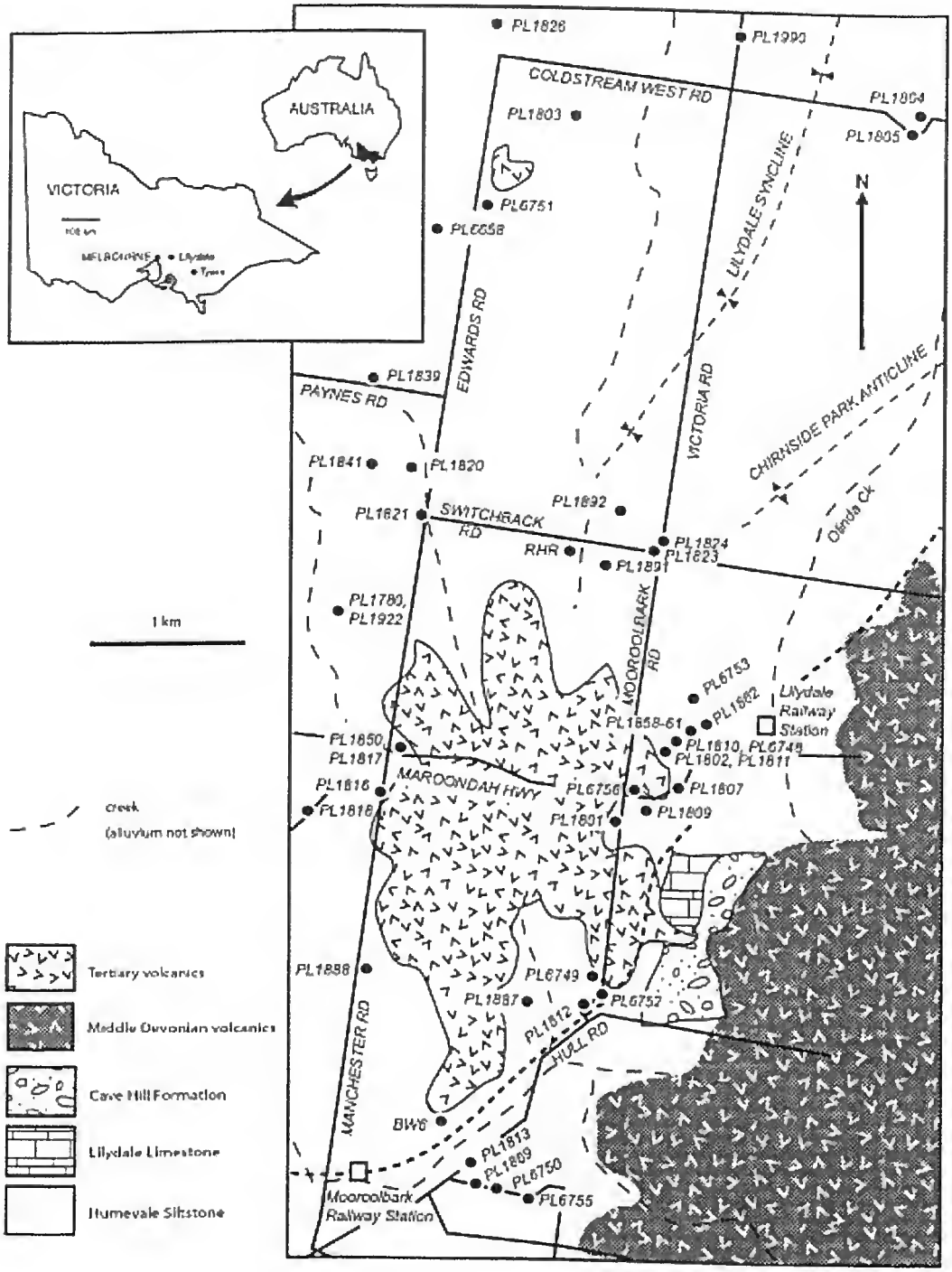


Fig. 1. Fossil localities in the Lilydale area. Geology follows VandenBerg (1970), Garratt (1972) and Wall et al. (1995). AMG gridlines and coordinates shown.

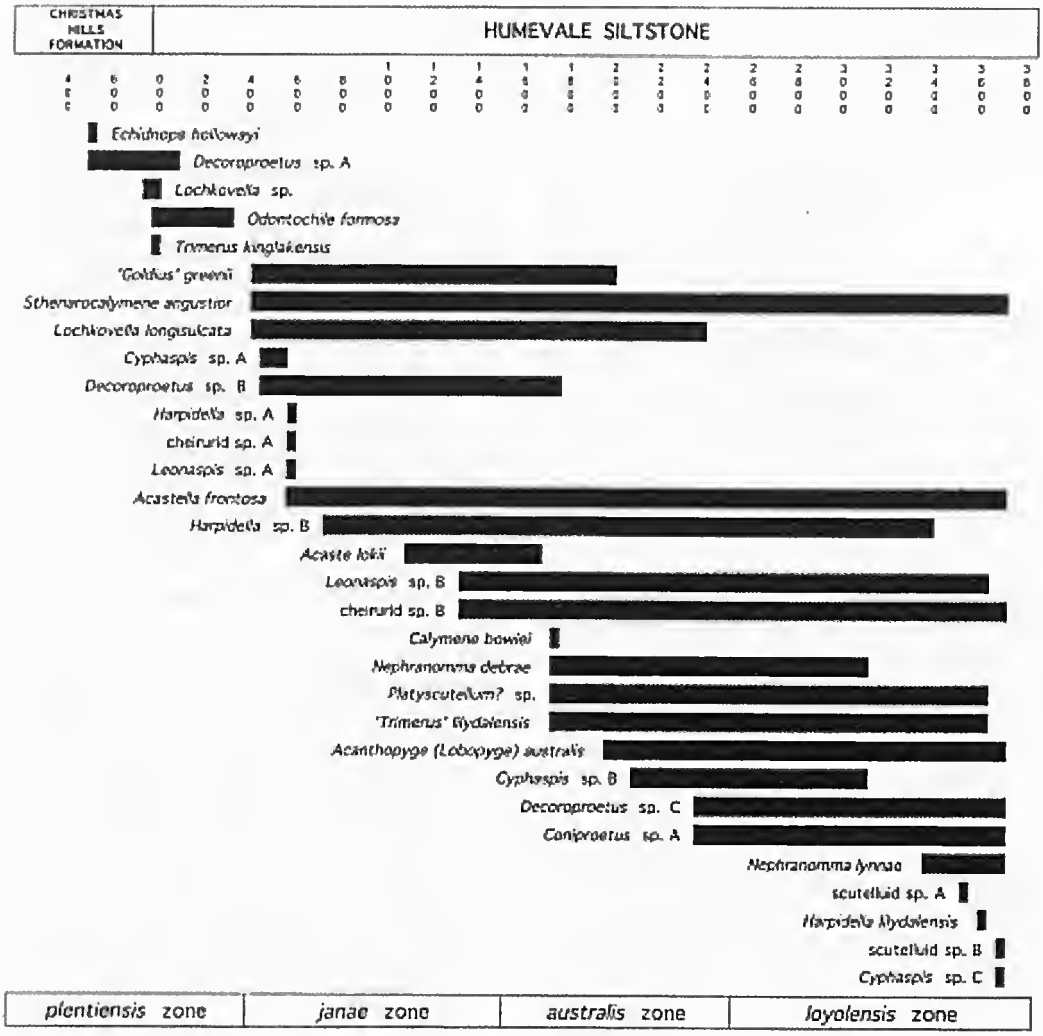


Fig. 2. Stratigraphic distribution of trilobites from the Christmas Hills-Lilydale sequence, in order of first appearances.

Coopers Creek include *S. angustior*, '*Goldius*' *cresswelli* Chapman, 1915, *Dicranurus* sp. and indeterminate proetid, aulacopleurid and lichid species.

BIOSTRATIGRAPHY, CORRELATION AND AGE

The trilobite fauna of the Humevale Siltstone occurs with an abundant brachiopod fauna, represented by at least 75 species (Garratt 1983: Fig. 5) and spanning four of the brachiopod assemblage zones described by Garratt (1983) and Garratt & Wright (1988) including the *Notoparmella plentiensis* Assemblage Zone (ranging up to the 400 m horizon), the *Boucotia janae* Assemblage Zone (ranging from the 400 m to the 1 500 m horizon), the *Boucotia australis* Assemblage Zone (ranging from the 1 500 m to the 2 500 m horizon) and the *Boucotia loyolensis* Assemblage Zone (ranging up from the 2 500 m horizon). Deriving age constraints from various brachiopod taxa and from graptolite, daeryoconarid and conodont faunas from other areas, Garratt & Wright correlated the base of the *janae* zone with the Siluro-Devonian boundary, and correlated the *australis* zone with the late Lochkovian *Monograptus*

Brachiopod and trilobite taxa represented in the upper Boola Siltstone at Tyers	Stratigraphic range at Lilydale (metres above base of Humevale Siltstone)		
TRILOBITES			
Lochkovella longisulcata	455	to	2400
Sthenarocalymene angustior	455	to	3800
BRACHIOPODS			
Lissatrypa lenticulata	50	to	3720
Plectodonta bipartita	300	to	3620
Cymostrophia euglyphoides	455	to	3720
Strophonella gypsiandica	455	to	2600
Eospirifer easteyi	500	to	3720
Spinatrypa fimbriata	540	to	3800
Notoleptaena clophera	560	to	3720
Maorostrophia kablei	600	to	3800
Boucotia australis	1150	to	3620
'Strophochonetes' cresswelli	1500	to	3720
Notanoplia philipi	1600	to	2950
Hysterolites lilydalensis	1700	to	3800
Schizophoria sp. nov. A.	1700	to	3720
Leptostrophia affinitata	2580	to	3720

Fig. 3. List of trilobite and brachiopod taxa common to the Tyers and Lilydale sequences, and their stratigraphic ranges at Lilydale.

hercynicus graptolite Biozone. They correlated the base of the *loyolensis* zone with the Lochkovian-Pragian boundary; although elsewhere Garratt (1983: 86) assigned the lower horizons of the *loyolensis* zone at Lilydale to the late Lochkovian. From these age estimates, *L. longisulcatus* ranges through the early and late Lochkovian, but excluding the earliest and latest Lochkovian.

The lithology and fauna of the Boola Formation were described in detail by Philip (1962). Problems regarding the nomenclature and correlation of strata currently referred to the Boola Formation and the overlying Coopers Creek Limestone were discussed by Mawson & Talent (1994). The age of the fauna occurring high in the Boola Formation is poorly constrained, with successive revisions providing younger age estimates. Philip (1960) considered that elements of the brachiopod fauna from the upper 45 m of the unit indicated a Ludlow age but, following the revision of indicator taxa in Belgium (Boucot 1960), Philip (1962) dated the assemblage as early Lochkovian. Savage (1973) correlated the fauna with the early Lochkovian *Gypidula pelagica* brachiopod Biozone. Garratt (1983) assigned the fauna to the *australis* zone, inferring a late Lochkovian age, although he noted the presence of *Lissatrypa lenticulata*, considered an index species of the *loyolensis* zone elsewhere. Mawson & Talent (1994) suggested that the *australis* zone ranged into the lower parts of the *sulcatus* zone (earliest Pragian). A minimum age of the Boola Formation fauna is constrained by conodont assemblages from the base of the overlying Coopers Creek Limestone, correlated by Mawson & Talent with the upper part of the *Eognathodus sulcatus* conodont Biozone (early Pragian).

In considering the ranges of the 16 brachiopod and trilobite species that co-occur in the Lilydale fauna and the Tyers fauna, the strongest similarity of the Tyers fauna is with the faunal succession ranging in the 1 700 m – 2 400 m and 2 580 m – 2 600 m intervals of the Humevale Siltstone at Lilydale, in which 15 of the 16 species common to both sequences are represented (Fig. 3). Emphasis on the last appearance of *Lochkovella longisulcata* suggests correlation with the lower interval. Unfortunately, this broad biostratigraphic correlation of the faunas is of limited significance in the age estimate of the Tyers fauna, as the age of the Humevale Siltstone fauna also remains poorly constrained. Despite the recently revised generic assignments of taxa represented at Lilydale (Talent et al. 2001), limited reliance can be placed on age constraints derived from the stratigraphic ranges of individual brachiopod and trilobite genera. Specifically, several genera considered by Brice *et al.* (2000) and Chlupáč et al. (2000) to be significant in the recognition of stage boundaries occur at Lilydale, but are anomalous with respect to their documented ranges. There is a greater degree of accord in the age suggested by trilobite species considered closest to those at Lilydale. The trilobite *'Trimerus' lilydalensis* Gill, 1949 (appearing at the 1 755 m horizon) belongs to a species group ranging no lower than the late Lochkovian elsewhere, and most closely resembles the poorly known late Lochkovian *'Digonus' bostoviensis* Tomczykowa, 1975 from Poland. *Lochkovella longisulcata* (last appearance at the 2 400 m horizon) most closely resembles the type species *L. misera* (Barrande, 1852) from the late Lochkovian-basal Pragian of Europe. Shergold (1968) compared his new species *Acastella frontosa* (ranging 550 m – 3 700 m interval) with *A. patula* Hollard, 1963 from the early Lochkovian of Morocco, and compared specimens of *Acaste lokii* Edgecombe, 1993 (ranging 1 100 m – 1 700 m interval) with *A. dayiana* Richter & Richter, 1954 from the early Lochkovian of Germany. These comparisons support a late Lochkovian age for the 1 700 m-2 400 m interval of the Humevale Siltstone.

There has been ongoing debate on the nature of the boundary between the Boola Formation and the overlying Coopers Creek Limestone. Philip (1965, 1968) argued that sedimentary features at the base of the Coopers Creek Limestone indicated a significant hiatus with respect to the Boola Formation. However, Mawson & Talent (1994) reinterpreted these features as localised and cited other features to support the overall conformity of the units. Poor constraints on the age

of the Boola Formation accommodate these divergent interpretations of the nature of its upper boundary with the Coopers Creek Limestone at Tyers. The early Lochkovian and late Lochkovian age estimates suggest a earliest Pragian hiatus to underlying the base of the Coopers Creek Formation, whereas earliest Pragian age estimates support interpretation of the sequence as conformable. Perhaps the most compelling support for a late Lochkovian rather than early Pragian age for the Tyers fauna is provided not by faunal elements, but by close alignment of the suggested hiatus between the Boola Formation and the Coopers Creek Limestone with the 'pre-1A' eustatic regressive phase recognised across North America by Johnson & Sandberg (1988). This event is correlated with the *pesavis* zone-early *sulcatus* zone (latest Lochkovian-earliest Pragian) interval, and is documented elsewhere as the basal Pragian boundary event (Walliser *in* Weddige 1998; Chlupác & Kukal 1986).

SYSTEMATIC PALAEONTOLOGY

Trilobite specimens described here are preserved as internal and external moulds. For photography, internal moulds have been coated with colloidal graphite, external moulds have been prepared as latex peels, and all were whitened with ammonium chloride. Specimens housed in the Melbourne Museum are registered with the prefix NMV P. Trilobite localities cited in the text include localities registered at the Melbourne Museum (prefixed PL), Geological Survey of Victoria localities (prefixed GSV), G. Sweet localities (prefixed Y or YF) and E. D. Gill localities (prefixed G). These and other localities are mapped in Gill (1940, 1945), VandenBerg (1970), Garratt (1977) and Wall *et al.* (1995).

Order Phacopida Salter, 1864
Suborder Phacopina Richter, Richter & Struve, 1959
Superfamily Phacopoidea Hawle & Corda, 1847
Family Phacopidae Hawle & Corda, 1847
Subfamily Phacopinae Hawle & Corda, 1847

Genus ***Lochkovella*** Chlupác, 1972

Type species. Phacops miser Barrande, 1852 from the Lochkov Formation (Lochkovian, *hercynicus* Zone, Early Devonian), Lochkov, Czech Republic.

Species assigned. Reedops deckeri Delo, 1935; *Ananaspis ekphymus* Jones, Hall, Wright & Carr, 1986; *Phacops fecundus minor* von Gaertner, 1930; *Phacops grimbergi* Frech, 1888; *Phacops (Phacops?) hanusi* Chlupác, 1977; *Phacops heritschi* von Gaertner, 1930; *Acaste longisulcatus* Shergold, 1968; *Phacops (Phacops?) velcs* Chlupác, 1972; *Kainops* sp. cf. *ekphymus* (*in* Ebach 2002); *Reedops* sp. nov. (*in* Holloway *in* Jell & Holloway 1983).

Range. Ludlow-Pragian.

Revised diagnosis. Glabella moderately convex, with front of glabella overhanging anterior border in dorsal view. Preoccipital ring as high as glabella anterior to L1. S2-S3 shallow to moderately deep. Eye placed with anterior margin adjacent to lateral border furrow. Glabellar ornament variable, ranging between moderately-sized tubercles to coarse granulation. Coarse to fine granulation on entire exoskeleton. Vincular furrow of variable depth, lateral notching indistinct. Hypostome inflated with middle furrow poorly defined, posterior border of moderate length. Pygidium with 6-7 deep pleural furrows that are uniform in depth to border, posterior furrows not markedly shallowed; interpleural furrows a well-defined incision, reaching border.

Discussion. Chlupác (1972) erected *Lochkovella* to accommodate species previously assigned to *Denckmannites*, restricting the latter to the type, *D. volborthi* (Barrande, 1852). Campbell (1977) regarded *Lochkovella* as a subgenus of *Denckmannites*, noting that both taxa share relatively narrow axial and wide pleural proportions that distinguish them from most other phacopids. Chlupác (1977) noted the rich segmentation of the pygidia shared by the two genera, and suggested possible derivation of *Lochkovella* from *Denckmannites*. This view was shared by Campbell, who considered the main difference between the groups to be the continuous anterior cephalic border of the latter. Chlupác (1977) listed further differences, including the greater convexity and forward projection of the glabella of *Lochkovella*, as well as its shorter hypostome and more distinct interpleural furrows. The differences between *Lochkovella* and *Denckmannites* are considered here to be profound and to support the full generic status of *Lochkovella*. *Denckmannites* is characterised by an unusually narrow glabella and an extraordinarily narrow pygidial axis (far narrower than those of *Lochkovella*), and large L1. Rich pygidial segmentation in the genera is manifestly different, in *Denckmannites* being expressed by a high number of pleural furrows (8 to 9) but in *Lochkovella* by well-

defined interpleural furrows (5 to 7). In addition, though the length of the eye is short in both *Lochkovella* and *Denckmannites*, the visual surface is differently developed, being highly reduced in *D. volborthi* but normally developed in *Lochkovella*. The similarities between these genera have been overstated and do not signify a close relationship. Rather, the specialised morphology of *Denckmannites* is analogous to that of other deep-water phacopids and reflects no more than adaption to the environment. Morphoclines involving eye length, pygidial segmentation and glabellar development recognised by Chlupác between *Denckmannites*, *Lochkovella* and *Reedops* are based on very generalised characters and do not indicate ancestor-descendant relationships as suggested by Campbell and Chlupác.

The concept of *Lochkovella* described in the revised diagnosis here is much wider than that of Chlupác (1977), and embraces a number of species previously assigned to *Reedops*, *Ananaspis*, *Phacops* and *Kainops*. *Lochkovella* differs from *Reedops* in having strongly expressed cephalic ornament that often extends over the entire exoskeleton, distinct S2-S3, and a lower cephalic length/width ratio (0.59 in *L. misera*; cf. 0.65-0.72 in *Reedops*). Chlupác described the glabella of *Lochkovella* as overhanging the anterior border, as in *Reedops*, although in glabellar profile the latter can be distinguished by its stronger inflation and, in some species, its more forward projection. In pygidial features *Lochkovella* can be easily distinguished from *Reedops* by the more robust appearance of the latter, being proportionally narrower and with a wider and more inflated axis, and with pleural furrows shallowing abruptly posteriorly with very weak to effaced interpleural furrows. Species previously assigned to *Reedops* include the Lochkovian *R. deckeri* Delo, 1935 from Oklahoma. Ormiston (1968) excluded *deckeri* from *Reedops* on the basis of its medially distinct vincular furrow. The depth of S2 and S3, the extensive granulate ornament and the depth and uniformity of pygidial pleural and interpleural furrows are also considered here as significant in distinguishing the species from that genus and in supporting assignment to *Lochkovella*. Similar features indicate that the closely comparable *Reedops* sp. nov. of Holloway *in* Jell & Holloway (1983) belongs to *Lochkovella*. The species occurs stratigraphically below *L. longisulcata* in the lowermost 100 m of the Humevale Formation at Christmas Hills. Associated faunal elements correlate with the *plentiensis* zone, considered here to span the late Ludlow-Pridoli. The species is distinguished in having a glabellar ornament of finer granules that extend, with little change in size or density, over the entire exoskeleton.

Although Campbell (1977) and Chlupác (1977) also suggested possible derivation of *Lochkovella* from *Ananaspis*, recognising strong resemblances in pygidial morphology, there has been very little other consideration given to the relationship between *Ananaspis* and *Lochkovella*. Chlupác did not explicitly compare *Lochkovella* with *Ananaspis*, and Campbell noted only that the glabellar shape of *Lochkovella* is more similar to *Ananaspis* than to *Reedops*. Ramsköld & Werdelin (1991) made no reference to *Lochkovella* in their cladistic analysis of Silurian-Early Devonian phacopids. In overall cephalic and pygidial morphology *Lochkovella* and *Ananaspis* are very similar, and the separation of the genera is not straightforward. Characters considered of significance in distinguishing *Ananaspis* include the presence of vincular notching (indistinct in *Lochkovella*), more proximally and higher-placed eyes (antero-laterally placed eyes in *Lochkovella*), a librigenal field separating the eye from the lateral border furrow (absent in *Lochkovella*) and more deeply incised interpleural furrows (shallower in *Lochkovella*). Emphasis on the lateral notching of the vincular furrow and the proximal placement of the eyes is justified by their conservative expression in presumably descendant groups of *Ananaspis* including *Paciphacops* and *Echidnops*. Morphology of the hypostome is another way of distinguishing the genera, although information is available for few species; the hypostome of *L. misera* exhibits a long posterior border, whereas in *A. fecundus* (and *Echidnops* and *Paciphacops*) it exhibits a short posterior border.

Species previously assigned to *Ananaspis* include the Lochkovian *A. ekphymus* Jones, Hall, Wright & Carr, 1986 from Bungonia, New South Wales. Ramsköld & Werdelin (1991) considered *A. ekphymus* to be conspecific with *Paciphacops (Paciphacops) microps* Chatterton, Johnson & Campbell, 1979 from the Pragian of Wellington, New South Wales, nominated as the type species of their new genus *Kainops*. However, *ekphymus* can be distinguished in having much denser and more uniformly sized cephalic and post-cephalic tuberculation, a vincular furrow that is almost indistinct medially, and a shorter eye and longer postocular genae (postocular length/eye length 0.6 in *ekphymus*; cf. 0.5 in *microps*). These differences are in accord with its assignment to *Lochkovella*. Following Ebach (2002), *ekphymus* is maintained here as an independent species. Ebach documented a species close to *ekphymus* from the Lochkovian-?Pragian at Cobar, New South Wales. The species differs from *ekphymus* in having much smaller cephalic tubercles and an even longer postocular genal length (eye length/postocular

genal length 0.7-1.0).

Species previously assigned to *Phacops* include two Pragian Czech species described by Chlupác (1977) as *Phacops (Phacops?) hamusi* and *P. (P?) veles*. Chlupác considered that these species represent morphologies intermediate between *Ananaspis* and *Phacops* and show some similarities to *Reedops*, and they were more recently placed in *Kainops* by Ramskold & Werdelin (1991). The finely tuberculate ornament of the exoskeleton, the well-defined pygidial segmentation and the antero-lateral placement of the eye indicate assignment to *Lochkovella*. In the low contrast between cephalic and post-cephalic ornament, these species are closest to *L. deckeri* and the species from Cobar and Christmas Hills.

Species previously assigned to *Lochkovella* by ChlupáC (1977) but excluded here include two species figured by Alberti (1970), *Phacops (Reedops)* sp. A aff. *akouchensis* (G. & H. Termier, 1950) and *Phacops (Reedops)* sp. B aff. *akouchensis*, both from Morocco. With further material Alberti (1983) redescribed these as species of *Phacops (Prokops)*. *Deuckmannites rutherfordi* Sherwin, 1968 from the Late Silurian Wallace Shale of New South Wales is also excluded from *Lochkovella*, differing from assigned species in having strongly defined notches on the vincular furrow.

Lochkovella longisulcata (Shergold, 1968)

Fig. 4A-S, Fig. 5A-S

1876 *Phacops (Portlockia) fecundus* (Barrande); McCoy, p. 15-16, pl. 22, figs 8-9; pl. 23, figs 2-3, *non* pl. 23, figs 1, 4-6 (= *Nephranomma debrae* Sandford, 2003).

1896 *Phacops sweeti* Etheridge & Mitchell, p. 497 (*non* figs = *Nephranomma sweeti* Etheridge & Mitchell, 1896).

1915 *Phacops crossleii*; Chapman, p. 168, pl. 15, fig. 15 *non* fig. 14 (= *Acaste lokii* Edgecombe, 1993)

1938 *Phacops fecundus*; Gill, p. 170 (pars).

1940 *Phacops fecundus* McCoy *non* Barrande; Gill, p. 250 (pars).

1951 *Phacops* sp. nov.; Gill, p. 31 (pars).

1968 *Acaste longisulcata* Shergold; p. 20, pl. 4, figs 7-8 *non* pl. 5, figs 1-12 (= *Acaste lokii* Edgecombe, 1993).

1996 *Ananaspis* sp. 1; Sandford, p. 220, pl. 26, figs A-H, *non* fig. 1 (=*Ananaspis* sp.)

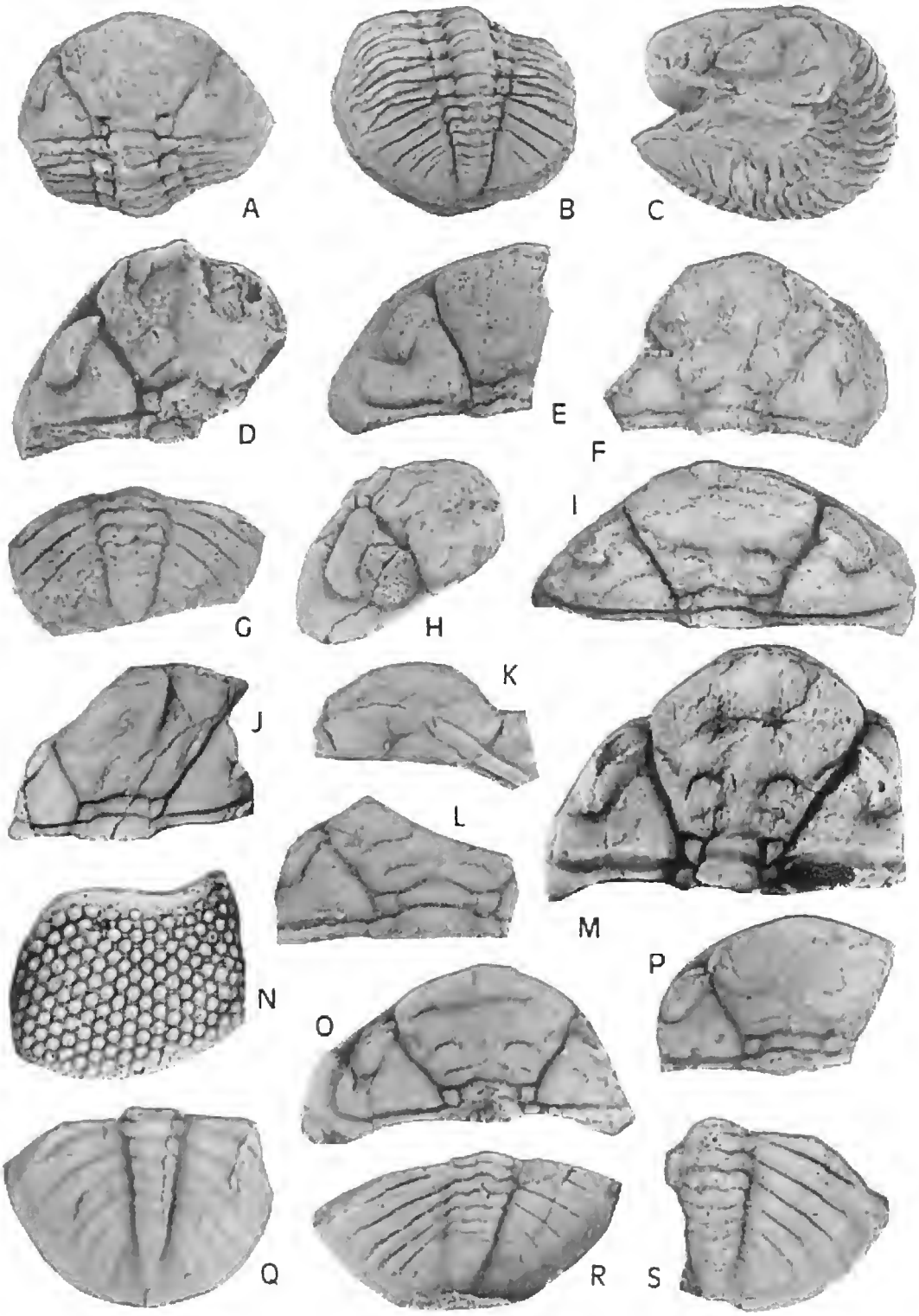
Type material. Holotype P12680 (pygidium, figured Chapman 1915: pl. 15, fig. 15, figured Shergold 1968: pl. 4, figs 7-8) from PL1820 (G20, *'Ruddocks Quarry'*), Chirnside Park. The paratypes of *Acaste longisulcata* including P25230-38, P25240 (all from PL1850 (G50, *'Black Springs Quarry'*), Chirnside Park form the type series of *Acaste lokii* Edgecombe, 1993.

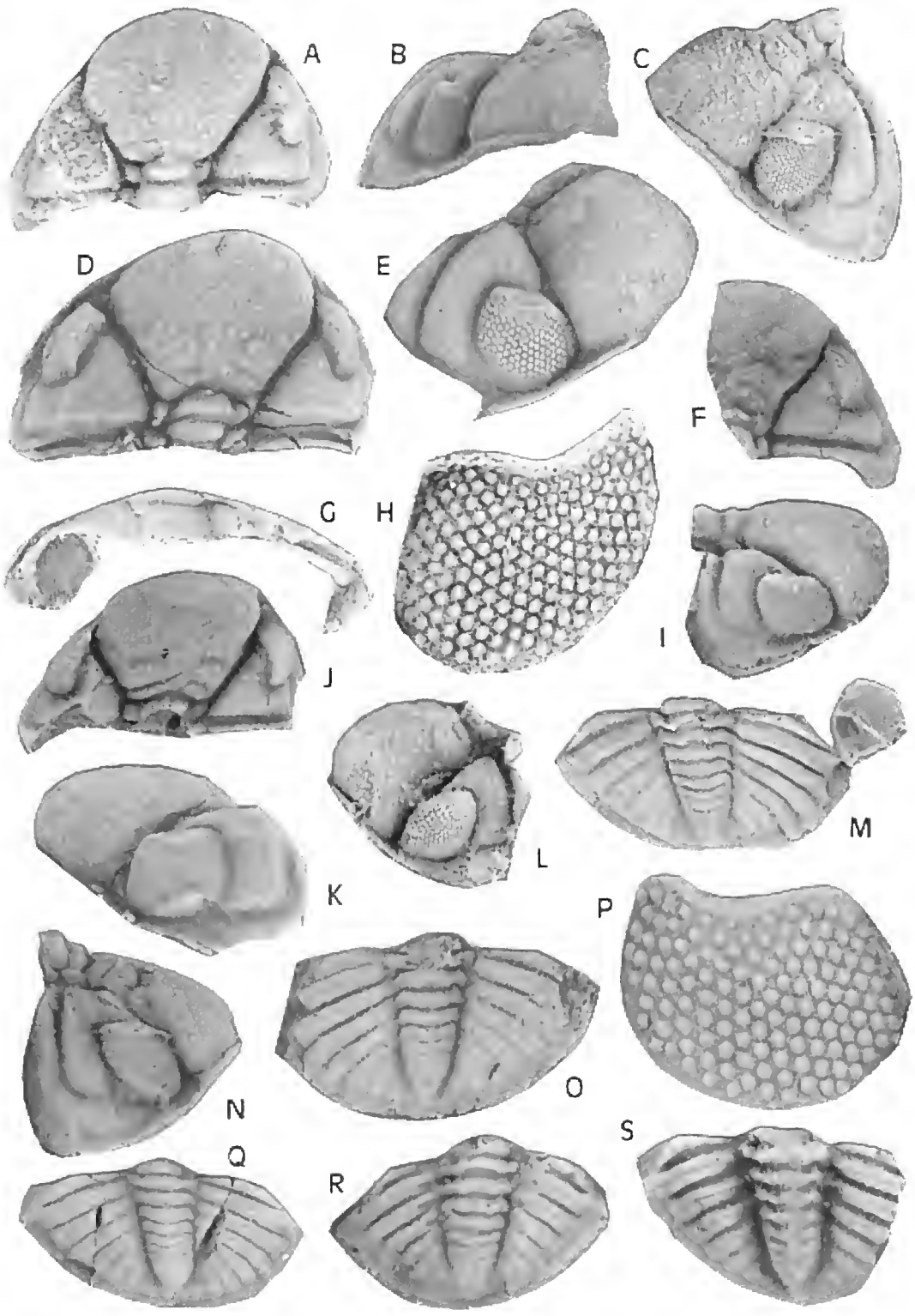
Figured specimens. P12118 (enrolled exoskeleton, figured McCoy 1876: pl. 23, figs 2, 3) from PL1804 (GSV B15, *'Section 12, Parish of Yering'*) Coldstream, considered by Gill (1940) the same locality as G4, *'Flowerfield* (or *Mic Blacks) Quarry'*. The cephalon and the pygidium figured by McCoy (1876: pl. 22, fig. 8, fig. 9 respectively) are missing but, from his illustrations they can also be confidently attributed to *L. longisulcata*.

Other material. 100 specimens: four exoskeletons, 39

Fig. 4. Lochkovella longisulcata (Shergold, 1968). A-C. P79123, enrolled exoskeleton, internal mould. A, dorsal view of cephalon x 1.0. B, lateral view x 1.25. C, dorsal view of pygidium x 1.0. D. Topotype P306868, cephalon, internal mould, dorsal view x 2.8. E. P12117, cephalon, internal mould, dorsal view x 1.6. F. P12118, cephalon, latex cast, dorsal view x 1.4. G. P306751, pygidium, internal mould, dorsal view x 1.8. H. P308933, cephalon, internal mould, oblique view x 1.75. I. P306919, cephalon, internal mould, dorsal view x 1.8. J. P308920, cephalon, latex cast, dorsal view x 3.0. K. P308925, cephalon, internal mould, ventral view (doublure) x 2.0. L. P306750, cephalon, latex cast, dorsal view x 2.3. M. P137147, cephalon, internal mould, dorsal view x 2.5. N. P308931, cephalon, latex cast, enlargement of eye x 9.0. O. P308919, cephalon, internal mould, dorsal view x 1.8. P. P308924, cephalon, internal mould, dorsal view x 2.2. Q. P308926, pygidium, latex cast, dorsal view x 2.4. R. P308928, pygidium, latex cast, dorsal view x 2.5. S. P308930, pygidium, latex cast, dorsal view x 2.5. A-G, I, M from the Humevale Siltstone. H, J-L, N, S from the Boola Formation.

Fig. 5. Lochkovella longisulcata (Shergold, 1968). A, I. P306914, cephalon, internal mould x 4.5. A, dorsal view. I, lateral view. B, C, F, H, N. P306875, cephalon. B, internal mould, anterior view x 2.75. C, latex cast, oblique view x 2.75. F, internal mould, dorsal view x 2.25.H, latex cast, enlargement of eye x 9.0. N, latex cast, lateral view x 2.75. D, E, M, P. Topotype P306864, partly enrolled exoskeleton. D, internal mould, dorsal view of cephalon and first thoracic segment x 3.3. E, latex cast, oblique view of cephalon x 4.0. M, internal mould, lateral view of cephalon x 4.4. P, latex cast, enlargement of eye x 12. G. Topotype P306867, cephalon, latex cast, ventral view (doublure) x 3.0. J. P306876, cephalon, internal mould, dorsal view x 3.7. K, L. P306872, cephalon. K, latex cast, oblique view x 5.0. L, external mould adjacent to large pygidium x 2.0. M. P306871, pygidium, internal mould, dorsal view x 2.0. O. P306916, pygidium, internal mould, dorsal view x 2.4. Q. Topotype P306865, pygidium, internal mould, dorsal view x 2.0. R. Holotype P12680, pygidium, internal mould, dorsal view x 2.5. S. P306877, pygidium, internal mould, dorsal view x 3.0. Humevale Siltstone.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S

cephala, one partly disarticulated thoracopygon, 56 pygidia. *Chirnside Park-Coldstream area:* Topotypes P306864-70 from PL1820. P137147-9, P140153 probably from PL1820. Unregistered specimen from PL1839 (G39, *'North of Ruddocks'*), Chirnside Park. P306890-1 from PL1817 (G17, *'Black Springs Cutting'*), Chirnside Park. P306916-17 from locality RHR (corner of Brentwoods and Rolling Hills Road), Chirnside Park. P26089 from PL1891 (G91), Chirnside Park. P79214, P306871-2, P306875-85, P306887-89 from PL6751, Chirnside Park. P306914-15 from PL1892 (G92), Chirnside Park. P306753-7, P306764 from PL1804 (YF, *'Yarra Flats'*). P306758 from PL1804 (Y, *'Yering'*). P12117, P306750-1, P306759 from PL1804 (GSV B15). P79123 from PL1804 or PL1805 (G5, *'Flowerfield Cutting'*), Coldstream. *Mooroolbark area*: P306919-20, P306986 from locality BW6 (corner of Winyard Drive and Baradine Road), Mooroolbark. *Tyers area:* P308919, P308953-4 from PL337, Tyers. P308920-8, P308939-50 from PL334, Tyers. P308929 (ex GSV 19377), P308952 from *'Tyers River'* (exact locality unknown). P308930-1 from *'Tyers'* (exact locality unknown). P308955 from *'near Tyers Quarry'* (exact locality unknown). *Coopers Creek area:* P308956 from PL1797, Coopers Creek. P308933-4 from *'Coopers Creek'* (exact locality unknown). P308951 from Evans Brothers Quarry, Coopers Creek.

Revised diagnosis. Lochkovella with anterior margin of glabella broadly rounded, with arc of curvature centred at about 0.25 cephalic length. Axial furrows weakly sinusoidal. Eye large for genus, length (exsag.) 0.37 times cephalic length, with midline placed opposite 0.53 cephalic length. Visual surface with 17-25 (mostly 18-21) lens files of up to 7-10 lenses per file and between 105-180 lenses. Postocular genal length (exsag.) 0.25 times cephalic length and 0.7 times length of eye (ranging to 0.2 times cephalic length and 0.4 times eye length in smaller specimens). Glabellar tuberculation comprising small, sparsely to densely distributed tubercles interspersed with dense ornament of granules, granulation coarser anteriorly, tubercles larger posteriorly. Palpebral area and postocular genae with subdued tuberculation. Vincular furrow indistinct medially, without notching laterally. Pygidium with 7-9 axial rings, 6-7 pleural ribs. Cephalic doublure and pygidium with ornament of fine granulation.

Description. Estimated maximum length 9 cm (based on specimen P79123). Cephalon roughly semicircular in dorsal outline, length about 0.56 times width. In anterior view glabella moderately convex, in lateral view, dorsal outline weakly convex posteriorly, strongly convex anteriorly, with anterior surface of glabella vertical. Glabellar length about equal to maximum width, anterior to occipital furrow expanding strongly forwards with maximum width about 0.6 times cephalic width and about 1.75 times occipital width, maximum glabellar width placed opposite 0.75 cephalic length. Occipital ring width 0.35 times cephalic width, length (sag.) 0.13 times cephalic length, with deep longitudi-

SPECIMEN	CEPHALIC LENGTH	LENS FORMULA		TOTAL LENSES	TOTAL FILES
P306872	5.5 mm	5 6 7 7 7 8 7 7 6 7 7 6 7 6 5 6 6 5 4 3 2		124 lenses	21 files
P306914	7 mm	. . 8 8 7 8 7 8 9 9 9 8 8 8 7 7 6 5 4 2		~140 lenses	20 files
P306876	7.5 mm	6 7 9 # # # # # # # #			21 files
P306867	9 mm	5 7 7 7 7 7 7 7 7 7 . . . . 6 6 4 3		~115 lenses	18 files
P306864	10 mm	5 7 7 8 8 8 8 8 8 8 8 8 8 7 7 6 5 4 1	right eye	129 lenses	19 files
		. . 8 8 8 9 9 8 8 8 8 6 6 6 7 6 5 4 2	left eye	~129 lenses	19 files
P306891	10 mm	4 6 6 6 7 7 7 8 8 8 7 7 6 6 5 5 2		105 lenses	17 files
P306868	11 mm	4 5 7 7 7 7 7 8 8 8 7 7 6 7 6 6 5 4		116 lenses	18 files
P306875	12 mm	5 7 8 9 9 # # # 9 9 9 8 9 9 9 8 7 7 5 5 3		165 lenses	21 files
P306919	13 mm	4 6 8 8 8 9 . . . . . 8 7 6 5 6 5 3 2		~135 lenses	20 files
P137149	13 mm	. . . . . 9 9 8 9 9 8 8 8 7 6 531			25 files
P308931		3 7 8 9 # 9 # 9 # 9 9 9 8 8 7 8 8 7 8 8 4 3 1		172 lenses	23 files
P306754	14 mm	6 7 7 8 9 9 9 # # # # # 9		~160 lenses	20 files
P306869	~15 mm	5 7 8 8 9 8 9 8 9 8 8 7 7 7 6 5 5 3		127 lenses	18 files
P137147	~15 mm	6 7 8 9 # # 9 # # 8 9 8 9 9 ? ? ? ? ? 7 6 5		~180 lenses	22 files
P306752	17 mm	. . . . . 8 9 8 9 8 8 7 8 8 . . . . 4 2			20? files

Table 1. Visual surfaces of specimens of *Lochkovella longisulcata* (Shergold, 1968).

nal furrow impressed into anterior margin of occipital ring opposite L1 and continuing across occipital ring as moderately impressed furrow, defining lateral occipital lobes, length (exsag.) of lobes about 0.5 times sagittal length of occipital ring. Medial section of occipital furrow transverse, and moderately impressed, short (sag.) on external surface, longer on internal moulds, lateral section offset (posteriorly), directed antero-laterally (at about 20° to the transverse) and deep. Medial section of pre-occipital ring with length about 0.07 times cephalic length, length 0.25 times width, in lateral view at same height as glabella anterior to L1. L1 isolated from preoccipital ring by longitudinal furrow, deep at anterior margin of ring and moderately impressed posteriorly. L1 quadrate, flat, length of L1 (exsag.) 0.1 cephalic length. L1-L1 0.9 times occipital width. S1 deep and transverse, continuous with preoccipital furrow that is shallow and long (sag.).

Eye oriented at about 20° to the saggital line. Visual surface with highly variable lens count, with 17-25 (mostly 18-21) lens files of up to 7-10 lenses per file and between 105-180 lenses in total (see Table 1). Palpebral lobe crescentic, length (exsag.) 0.3 times cephalic length, narrow (width at midlength about 0.2 times length), with prominent palpebral rim and distinct palpebral rim furrow, δ?δ 0.8 times cephalic width and 1.35 times glabellar width. Palpebral furrow moderately impressed, shallowing opposite palpebral midlength, continuous with deep postocular furrow. Sclera not raised. Anterior half of eye extending to librigenal border furrow, librigenal field poorly defined as a small depressed triangular area bounded by postero-lateral margin of eye, lateral border furrow and facial suture. Lateral border narrow and concave anteriorly, markedly widening posterior to midlength of eye, with shallow epiborder furrow extending to the point where the facial suture crosses the lateral margin. Cephalic doublure with sagittal length about 0.3 times cephalic length. Hypostomal suture transverse, with moderate median sag in anterior view.

Thoracic axial rings with strongly defined, quadrate, flat lateral nodes.

Pygidium lenticular in outline, with length about 0.5 times width, weakly convex. Axis raised, width 0.27 times pygidial width, moderately tapering, sides converging posteriorly at about 22°, reaching to 0.95 pygidial length, triangular terminal piece. First axial ring with well defined pseudo-articulating half-ring impressed into posterior margin, poorly defined on second and third rings, indistinct posteriorly. Interpleural furrows shallow but distinct. Pleural furrows deep and wide, shallowing abruptly adjacent to margin, lateral border furrow and border poorly defined. Axial rings with coarse granulation. Pygidial doublure narrow, steeply inclined laterally, sub-vertical posteriorly, strongly convex in section.

Glabellar tuberculation comprising small, sparsely to densely distributed tubercles interspersed with dense ornament of granules, granulation coarser anteriorly, tubercles larger posteriorly. Palpebral area and postocular genae with subdued tuberculation. Fine granulation on remainder of exoskeleton.

Remarks. McCoy's (1876) description of '*Phacops (Portlockia) fecundus* Barrande, 1846' from Coldstream is based predominantly on specimens of *Lochkovella longisulcata*, and he listed a number of characters that are in accord with its assignment to *Lochkovella* including the long postocular genal length, the weak glabellar tuberculation, the granular surface ornament and the definition of the pygidial pleural and interpleural furrows. Etheridge & Mitchell (1896) referred McCoy's Coldstream specimens together with specimens from Loyola to their new species *Phacops sweeti*. However, Gill (1938) considered that the high lens counts of the Loyola specimens (22 rows, up to 12 lenses per row) distinguished them from the Coldstream specimens. Gill (1951) considered the latter represented one and possibly two new species, conclusions confirmed by their subsequent assignment to *Nephranomma debrae* Sandford, 2003 and *L. longisulcata*. Gill pre-empted the assignment of McCoy's specimens to *Lochkovella* in noting the morphology was intermediate between *Reedops* and *Phacops*, and close to *R. deckeri*.

Lochkovella longisulcata is closest to *L. misera*. These species differ from the *deckeri* group in exhibiting a distinct contrast in the grade of cephalic and postcephalic ornament, a contrast stronger in *L. longisulcata*. In this respect these species are closest to *Ananaspis*. *Lochkovella longisulcata* further differs from the type species in having a slightly more broadly rounded glabellar anterior margin, sinusoidal rather than straight axial furrows; a larger eye (17-21, rarely 23-25 files of up to 7-10 lenses per file, see Table 1, cf. 13-14 files of up to 6 lenses per file in *L. misera*) that is more forwardly placed (anterior margin of eye opposite 0.7 rather than 0.65 cephalic length); glabellar tubercles that are slightly bigger and extend onto the genal areas, and finer interspersed granulation; and shallower pleural furrows posteriorly.

Variation within the populations assigned to *Lochkovella longisulcata* is considerable. Glabellar tuberculation ranges in density from sparse to dense and in size from small tubercles to coarse granules.

Tubercles on the smallest specimens are most prominent, as might be expected. More difficult to explain is the distinctly subdued ornament on specimens of both *L. longisulcata* and *Nephranomma debrae* in sandstone at PL1804 compared to specimens in siltstone at other localities; the differenecs appear to be real and cannot be attributed to preservation in a sandier matrix. Variation in glabellar ornament occurs between individuals from the same locality, but variations in eye size and lens arrangement appear to oeeur between populations from different loealities. Specimens from the Tyers-Coopers Creek area have slightly shorter eyes/longer postoeular genae than those from the Lilydale sequence, whereas those from the PL6751 (Coldstream) have somewhat longer eyes/shorter postocular genae than those from other loealities. As there are no other eonsistent differences in degree of tubereulation, eye lenticulation or pygidial segmentation that further distinguish the various populations of *L. longisulcata*, they are considered to refleet natural intraspecific variation.

Lochkovella longisulcata oecurs with *Nephranomma debrae* at several loealities between the 1 750 m and 2 400 m horizons of the Humevale Siltstone. The two speeies are similar in overall appearance, but can always be distinguished by the shorter postocular genal length and larger eye in *N. debrae*. In addition, in *N. debrae* the glabellar tubereules are generally coarser; its eyes have higher lens eounts (160-183 lenses in 10-11 files) and are plaeed more or less in exsagittal orientation; its cephalic doublure is more coarsely ornamented; and its pygidium is less deeply furrowed and only has five pleural furrows.

Four cephala erroneously doeumented from the Late Wenloek-Early Ludlow Yan Yean Formation and previously deseribed as *Ananaspis* sp. 1 (Sandford 1996) belong to *L. longisulcata*. The lithology and preservation of the speeimens most elosely matches that of the type loeality PL1820, (G20, *'Ruddocks Quarry'*) from where they were probably collected.

ACKNOWLEDGMENTS

The author is most appreciative of improvements to the manuscript suggested by Dr A. J. Wright (University of Wollongong) Dr Stephen Gallagher (University of Melbourne) and Dr David Holloway (Melboume Museum). The manuscript was prepared with support from a David Hay Postgraduate Award.

REFERENCES

Alberti, G. K.B., 1970. Trilobiten des jüngeren Siluriums sowie des Unter- und Mitteldevons. 2. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 525: 1-233.

Alberti, G. K.B., 1983. Trilobiten des jüngeren Siluriums sowie des Unter- und Mittel-Devons. 4. *Senckenbergiana lethaea* 64: 1-87.

Boucot, A.J., 1960. Lower Gedinnian brachiopods of Belgium. *Louvain Institut géologique Mémoire* 21: 283-324.

Barrande, J., 1846. *Notice préliminaire sur le Système silurien et les trilobites de Bohême*. C.L. Hirschfeld, Leipzig, vi + 97 pp.

Barrande, J., 1852. *Système silurien du centre de la Bohême. 1ère partie. Recherches palèontologiques, vol. 1. Crustacés, Trilobites*. Prague and Paris, 935 pp., 51 pls.

Brice, D., Carls, P., Cocks, L.R.M., Copper, P., Garcia-Alcalde, J.L., Godefroid, J. & Racheboeuf, P.R., 2000. Braehiopoda, In *Subcommision on Devonian Stratigraphy. Fossil groups important for boundary definition*, P. Bultynek, ed., *Courier Forschungsinstitut Senckenberg* 220, 65-86.

Campbell, K.S.W., 1977. Trilobites of the Haragan, Bois d'Arc and Friseo formations (Early Devonian) Arbuekle Mountains Region, Oklahoma. *Bulletin of the Oklahoma Geological Survey* 123: 1-221.

Chapman, F., 1915. New or little-known Vietorian fossils in the National Museum. Part 18. Some Yeringian trilobites. *Proceedings of the Royal Society of Victoria* 28: 157-171.

Chatterton, B. D. E., Johnson, B. D. & Campbell, K. S. W. 1979. Silieified Lower Devonian trilobites from New South Wales. *Palaeontology 22*, 799-837.

Chlupác, I., 1972. New Silurian and Devonian phacopid trilobites from the Barrandian area (Czechoslovakia). *Casopis pro mineralogii a geologii* 17: 395-401.

Chlupác, I., 1977. The phaeopid trilobites of the Silurian and Devonian of Czechoslavakia. *Rozpravy Ústredního Ústavu Geologického* 43: 1-172.

Chlupác, I., Feist, R. & Morzadec, P., 2000. Trilobites and standard Devonian stage boundaries. In *Subcommision on Devonian Stratigraphy. Fossil groups important for boundary definition*. Bultynck, P. (ed.). *Courier Forschungsinstitut Senckenberg* 220, 87-98.

CHLUPÁC, I. & KUKAL, Z. 1986. Reflection of possible global Devonian events in the Barrandian area, C. S. S. R., In *Global Bioevents. Lecture Notes in Earth Sciences* 8, Walliser, O. H. (ed). Springer, Heidelberg, 171-179,.

DELO, D.M., 1935. A revision of the phacopid trilobites. *Journal of Paleontology* 9: 402-420.

EBACH, M.C., 2002. Lower Devonian trilobites from Cobar, New South Wales. *Records of the Western Australian Museum* 20: 353-378.

EDGECOMBE, G.D., 1993. Silurian acastacean trilobites of the Americas. *Journal of Paleontology* 67: 535-548.

ETHERIDGE, R. & MITCHELL, J., 1896. The Silurian trilobites of New South Wales, with references to those of other parts of Australia. Part 3. The Phacopidae. *Proceedings of the Linnean Society of New South Wales* 20: 486-511.

ETHERIDGE, R. & MITCHELL, J., 1917. The Silurian trilobites of New South Wales, with references to those of other parts of Australia. Part 6. The Calymeneidae, Cheiruridae, Harpeidae, Bronteidae, & c., with an appendix. *Proceedings of the Linnean Society of New South Wales* 42: 480-510.

FRECH, F., 1888. Über das Devon der Östalpen, nebst Bemerkungen über das Silur und einem paläontologischen Anhang. *Zeitschrift der Deutschen geologischen Gesellschaft* 39: 44.

GAERTNER, H.R. von., 1930. Silurische und tiefunterdevonische Trilobiten und Brachiopoden aus den Zentralkarnischen Alpen. *Jahrbuch Preussischen geologischen Landesanstalt zu Berlin* 51: 188-249.

GARRATT, M.J., 1977. *Kinglake 1:63,000 geological map*. Department of Mines, Melbourne.

GARRATT, M.J., 1983. Silurian and Devonian biostratigraphy of the Melbourne Trough, Victoria. *Proceedings of the Royal Society of Victoria* 95: 77-98.

GARRATT, M. J. & WRIGHT, A.J., 1988. Late Silurian to early Devonian biostratigraphy of southeastern Australia, In *Devonian of the World. Proceedings of the Second International Symposium on the Devonian System, Calgary, Canada. Volume III. Paleontology, Paleoecology and Biostratigraphy.* McMillan, N. J., Embry, A. F. & Glass, D. J. (eds). Memoir 14. Canadian Society of Petroleum Geologists, Calgary, Alberta, Canada, 647-662.

GILL, E.D., 1938. Yeringian trilobites. *Victorian Naturalist* 54: 167-171.

GILL, E.D., 1940. The Silurian Roeks of Melbourne and Lilydale: a diseussion of the Melbournian-Yeringian boundary and assoeiated problems. *Proceedings of the Royal Society of Victoria* 52: 249-261.

GILL, E.D., 1945. Trilobita of the Family Calymenidae from the Palaeozoie rocks of Victoria. *Proceedings of the Royal Society of Victoria* 56: 171-186.

GILL, E.D., 1948. A gens of dalmanitid trilobites. *Journal and Proceedings of the Royal Society of New South Wales* 82: 16-24.

GILL, E.D., 1949. Some Australian homalonotid trilobites. *Proceedings of the Royal Society of Victoria* 61: 61-74.

GILL, E.D., 1951. Revision of McCoy's 'Prodromus' types from the Lilydale and Killara districts of Victoria. *Proceedings of the Royal Society of Victoria* 63: 31-38.

HAWLE, I. & CORDA, A.J.C., 1847. Prodrom einer Monographie der böhmischen Trilobiten. J. G. Calve, Prague, 176 pp.

HOLLARD, H., 1963. Les *Acastella* et quelques autres Dalmanitacea du Maroe présaharien. Leur distribution verticale et ses consequenees pour l'étude de la limite Silurien-Dévonien. *Notes et Mémoires du Service Géologique du Maroc* 176: 1-66.

HOLLOWAY, D.J. & NEIL, J.V., 1982. Trilobites from the Mount Ida Formation (Late Silurian-Early Devonian), Victoria. *Proceedings of the Royal Society of Victoria* 94: 133-154.

JELL, P.A. & HOLLOWAY, D.J., 1983. Devonian and ?Late Silurian palaeontology of the Winneke Reservoir site, Christmas Hills, Victoria. *Proceedings of the Royal Society of Victoria* 95: 1-21.

JOHNSON, J.G. & SANDBERG, C.A., 1988. Devonian eustatic events in the western United States and their biostratigraphic responses, In *Devonian of the World. Proceedings of the Second International Symposium on the Devonian System, Calgary, Canada. Volume III. Paleontology, Paleoecology and Biostratigraphy.* N.J. McMillan, A.F. Embry Jr & D.J. Glass, eds, Memoir 14. Canadian Society of Petroleum Geologists, Calgary, Alberta, Canada, 171-178.

JONES, B.G., HALL, C.G., WRIGHT, A.J. & CARR, P.F., 1986. The geology of the Bungonia-Windellama area, New South Wales. *Proceedings of the Linnaean Society of New South Wales* 108: 267-286.

MCCOY, F., 1876. *Prodromus of the palaeontology of Victoria; or figures and descriptions of Victorian organic remains. Decade 3.* Geological Survey of Victoria, Melbourne, 40 pp., pls 21-30.

MAWSON, R. & TALENT, J.A., 1994. Age of an Early Devonian carbonate fan and isolated limestone clasts and megaclasts, east-central Victoria. *Proceedings of the Royal Society of Victoria* 106: 31-70.

ORMISTON, A.R., 1968. Lower Devonian trilobites of Hereynian type from the Turkey Creek inlier, Marshall County, south-central Oklahoma. *Journal of Paleontology* 42: 1186-1199.

PHILIP, G.M., 1960. Victorian Siluro-Devonian faunas and correlations. *International Geological Congress, Report of Twenty-first Session, Norden* 7: 143-157.

PHILIP, G.M., 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 123-246.

PHILIP, G.M., 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 79: 95-117.

PHILIP, G.M., 1968. Late Silurian-early Devonian relationships in the central Victorian and western Tasmanian clastic sequences, Australia. In *International Symposium on the Devonian System, Calgary, volume 2.* Oswald, D. H. (ed.). Alberta Society of Petroleum Geologists, Calgary, 913-920.

RAMSKÖLD, L. & WERDELIN, L., 1991. The phylogeny and evolution of some phacopid trilobites. *Cladistics* 7: 29-74.

RICHTER, R. & RICHTER, E., 1954. Die Trilobiten des Ebbe-Sattels und zu vergleichende Arten (Ordovizium, Gotlandium/Devon). *Abhandlungen der Senckbergischen, Naturforschenden Gesellschaft,* 488: 1-76.

RICHTER, R., RICHTER, E. & STRUVE, W., 1959. Suborder Phacopina. In *Treatise on invertebrate paleontology, Part O, Arthropoda 1.* R.C. Moore, ed., Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas,454-461

SALTER, J.W., 1864. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. Part 1. *Monograph of the Palaeontographical Society*, 1-80.

SANDFORD, A.C., 1996. *Silurian trilobites of central Victoria.* MSc thesis, University of Melbourne, 320 pp.

SANDFORD, A.C., 2003. A revision of *Nephranomma* Erben, 1952 (Trilobita, Phacopidae), with new species from the Early Devonian of Victoria, Australia. Phacopidae of Victoria, Part 2. *Special Papers in Palaeontology* 70: 309-329.

SAVAGE, N.W., 1973. Lower Devonian biostrat-igraphic correlation in eastern Australia and western North America. *Lethaia* 5: 341-348.

SHERGOLD, J.H., 1968. On the occurrence of the trilobite genera *Acaste* and *Acastella* in Victoria. *Proceedings of the Royal Society of Victoria* 81: 19-30.

SHERWIN, L., 1968. *Deuckmannites* (Trilobita) from the Silurian of New South Wales. *Palaeontology* 11: 691-6.

TALENT, J.A., GRATSIANOVA, R.T. & YOLKIN, E.A., 2001. Latest Silurian (Pridoli) to Middle Devonian (Givetian) of the Asia-Australia hemisphere: rationalisation of brachiopod taxa and faunal lists; stratigraphic correlation chart. *Courier Forschungsinstitut Senckenberg* 236: 1-121.

TERMIER, G. & TERMIER, H. 1950. *Paléantologie marocaine. Tome 2. Invertébrés de l'ére primaire. Fascicule 4. Annélides, arthropods, echinodermes, canularides et graptolites.* Hermann & Cie, Paris, 279 pp.

TOMCZYKOWA, E. 1975. The trilobite subfamily Homalonotinae from the Upper Silurian and Lower Devonian of Poland. *Acta Palaeontologica Polonica* 20: 1-46.

VANDENBERG, A.H.M., 1970. *Ringwood 1:63,000 Geological Map.* Department of Mines, Melbourne.

WALL, R., MAWSON, R., TALENT, J.A. & COOPER, B.J., 1995. Conodonts from an environmentally hostile context, the Lilydale Limestone (Early Devonian: Pragian) of central Victoria. *Courier Forschungsinstitut Senckenberg* 182: 371-387.

WEDDIGE, K. 1998. Devon-Korrelationstabelle. *Senckenbergiana lethaea* 77: 289-326.

Manuscript received 15 September 2002
Revision accepted 10 July 2003

LEJEUNEACEAE (HEPATICAE) OF VICTORIA; ADDITIONS AND A RESTITUTION.

DENIS J. CARR

17 Collings Street. Pearce.ACT 2607

CARR, DENIS J., 2004:12:04. Lejeuneaceae (Hepaticae) of Victoria; Additions and a restitution. *Proceedings of the Royal Society of Victoria* 116(2): 221-232. ISSN 0035-9211.

Six species of the genus *Lejeunea* are described from specimens collected in various Victorian localities during the mid 1950s. One, *L.fawcettiae* is new to Science and as far as is known, endemic to the State. An additional species, hitherto unknown to mainland Victoria is described and restored to its former subgeneric status. It is *Microlejeunea primordialis.* Novel characterisitcs of the widespread and variable species. *L. tumida* are described, including its gemmae and pseudo-perianths It is suggested that the very rare *L. mevicarii* of Inverness, Scotland is identical with *L tumida* and may have been introduced from Tasmania.

UNTIL the publication of Scott (1985) no single guide was available to the hepatics of Victoria The identification of specimens collected there required reference to a widely dispersed literature, or the treatments provided by Rodway (1916) of the Tasmanian species or those of NSW by Stephani and Watts (1914), (see also Cropper *et al* 1991).

Quite a few of the species occurring in both regions are not listed by Scott as occurring in Victoria. In addition, among the "missing" are some cosmopolitan "weedy" species which ought to occur in Victoria. One such is indeed recorded by Scott as having been found in East Gippsland. It is *Cololejeunea minutissima* (Sm.) Schiffner. This "aggressive epiphyte" (Schuster 1983: 590) occurs throughout the world as a series of closely related sub-species or species; its occurrence in the State could have been predicted as highly probable. Another (not yet recorded) is *Lejeunea flava* Sw., also regarded as a cryptogamic weed by Schuster (1983) who says that it (like *C. minutissima*) "tolerates salt spray and a considerable level of exposure to desiccation". It has been widely collected in NSW, often under the synonym *L. thymifolia* Nees. In Japan it occurs as a corticole in maritime locations in the warmer parts of that country (Mizutani 1961). According to Richards (1984: 1237) "it occurs in disturbed sites and may owe its cosmopolitan distribution to man". Another cosmopolitan species which could be found in Victoria is *Leptolejeunea elliptica* (L & L.) Steph. which occurs widely in Pacific countries to the north of Australia as well as in New Zealand.

This paper endeavours to rectify some of these lacunae in the flora of Victoria, also to restore *Microlejeunea primordialis,* which had been reduced to *Lejeunea* by Scott without advancing any reason. I am reliably informed , by Dr J.H.Ross (see Acknowledgments) that there have been no additions to the Lejeuncaceae of Victoria since the publication of Dr. Scott's monograph in 1985.

Vouchers of all specimens cited will be lodged with the National Herbarium of Victoria

METHODS

Samples of the specimens were mounted, first in water, for microscopical examination, then in glycerin-jelly with the addition of a little toluidine blue; the dye stains the cell walls and is useful in enhancing visualisation of delicate structures.

Specimens were photographed using Kodak T400 film in a Nikon photomicroscope. Thin sections were cut with a diamond knife of materials embedded in White's No 25 resin. Preparations were also photographed using a Nikon Coolpix digital camera, the images enhanced by Photoshop Elements software and printed using a Photosmart or a Cannon S100SP printer. Drawings were made from photographic prints.

(1) *Lejeunea flava* Sw. *Flora Indica occid.* p. 444. *L .thymifolia* Nees. *Syn. Hep.* p 372.

The following description is based on a specimen collected by myself and Mrs Carr (Carr and Carr 457) in April 1957 on a gully at Mait's Rest, near Apollo Bay, on Hordern Vale Road, Victoria. and another (Carr & Carr 3571) from the bark of a blackwood

tree near Tooronga, River, Noojee, Victoria.

Monoicous. creeping on the bark of *Hedycarya* and *Acacia melanoxylon* in association with mosses, and the liverworts *Frullania c.f. rostrata* and *Metzgeria c.f.densiseta.* In thin flat, yellowish-green patches. Stems up to 12 mm long, irregularly, but not pinnately branched. Leaves contiguous and patent, overlapping a little, divergent, the antical lobe somewhat convex, oblong to oval, 210 µm long, bluntly rounded at the apex, the margin entire, attached to the outer cortical merones of the stem, the base not overlapping it. At the leaf tip, it is bordered by small cells (14µm wide) with another row of small cells, sometimes incomplete. within it followed by one or two parallel longitudinal rows of larger cells (up to 23µm wide). The postical lobe not large, c. 80-100 µm long, 70 µm wide, strongly convex, the keel arched strongly and decurrent into the ventral part of the antical lobe. The basipetal edge of the antical lobe and the keel of the postical lobe meet in a deep sinus.The free margin of the postical lobe involute except at the apex, with a tooth, consisting of a single projecting cell, very close to the apex. Cells uniformly thin walled but with very small trigones (Fig. 4A) No ocelli. Oil bodies numerous, 8-25 per cell, very small, round, elliptical or vermiform. Underleaves orbicular, bifid, 220µm long and the same in width i.e about four times as wide as the stem (which is 50 µm wide), the margin entire (Fig. 1E). Sinus narrow, at a depth of 40% of the length of the underleaf, the acute to obtuse lobes not divergent, each tapering to a tip consisting of one or two cells. The base of the underleaf subcordate. The stem section shows 7 cortical cell rows surrounding 23 rows of much smaller medullary cell rows i.e. twice as many as in the Japanese specimens according to Mizutani (*loc. cit*). Rhizoids not scarce (cf. Mizutani,) sometimes forming "attachment organs" (Haftorgane) each consisting of the expanded tips of a fascicle of rhizoids. Perianth pyrifom 0.8mm long, 0.5mm wide terminating a short lateral, succeeded by one or two innovations (Fig. 1F). The beak short, consisting of groups, each about six cells. The ventral and lateral keels not prominent but extending more than half the length. The involucral leaves ovate-acuminate, 55µm long, the bractcole similar to the stem underleaves. Antheridia two to four on short lateral branches with two to six bracts, which are smaller than the leaves. The seta of the capsule very short, the c.16 elaters each 200µm. long with expanded tips, colourless, contorted, attached near the tips of the four valves, lacking internal spiral thickenings. The spores oval, 25µm wide, the extine finely punctate.

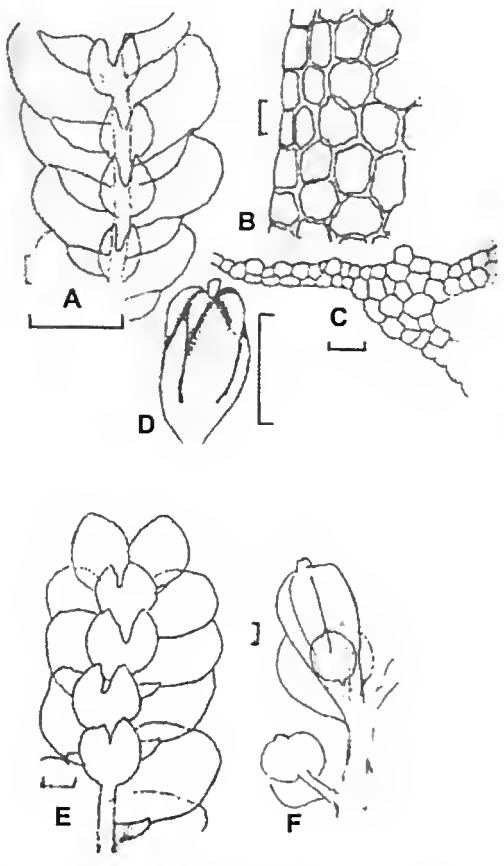


Fig 1. A-D. *L. cavifolia.* A. Portion of shoot. B. Cells near the edge of the leaf. C. Part of lobule with tooth. D, Perianth; E-F, *L. flava.* E, part of shoot. F. Perianth.
Scale bars A, E & F. 100µm. B & C, 10µm. D. 1mm.

Comment. The leaves of specimens from Killarney, Ireland are reported by McVicar (1926: 429) to be "occasionally shiny when dry". Certainly the Victorian plants do glisten when specimens are viewed in the dissecting microscope. This can be attributed perhaps to the large number of small oil bodies in each cell, or more likely to some light-reflecting property of the cell-walls since other species of *Lejeunea* with similar or even greater numbers of small oil bodies, e.g. *L. subelobata,* lack the shininess of *L. flava.* The result is to lend a rather golden iridescence to the appearance of the dry plant seen under a lens. It vanishes as soon as the plant is moistened, to be replaced by semi-translucency. Mizutani (1962: 200)

does not refer to this phenomenon in relation to the Japanese specimens.

(2) *Lejeunea cavifolia.* (Ehr) Lindb. *Acta. bot. Soc. Femnica* 1871: 43.
L. serpyllifolia, Libert, Ann Gen Sci Phys,6,1820: 374.

The following description is drawn up on the basis of a specimen collected by Mrs Carr and myself (Carr & Carr 255) at Lorne. Victoria, February 1955. Another specimen was collected February 1956 growing on tree branches in a beech gully at Beenak Victoria, (Carr & Carr 2562) together with *Radula buccinifera* and *Harpalejeunea laetitans.* Yet a third (Carr & Carr 1562) was collected on a fern gully in the Otway Ranges Victoria, epiphytic on large clumps of the moss *Ptychomnium aciculare.*

In dense, flat, dull olive-green patches on the bark of trees, stems 12-20mm long irregularly branched, the branches spreading widely to form plants almost as wide as long (Fig. 6E). Leaves very closely imbricate, (hence the synonym, from Latin *serpyllum,* wild thyme*)* patent, inserted at about 60 degrees to the stem (Fig. 1A), somewhat concave, ovate. 235μm long 130μm wide, rounded, or more rarely subacute at the apex, margin entire. The plants from Beenak had the leaves inserted at angles of 20-30 degrees to the stem, and were more closely imbricate and crowded giving the long stems a julaceous appearance.

The acropetal margin in antical view widely overlapping the stem. Leaf bordered by small cells each 12 μm wide (Fig. 1B). Cells becoming larger with distance from the margin, 25μm near the margin to 30μm in the centre of the leaf (Fig. 4B). Oil bodies small, numerous, ovoid to fusiform, 7-25 per cell. Cell walls uniformly thin, no or only minute trigones.

Postical lobe small, (Fig. 1A & 1C) 250 μm long, 100 μm wide, inflated, the free margin involute except near the apex, with a single blunt 1-celled tooth.

Underleaves large, (Fig. 1A) overlapping, 300 μm long and the same in width, three to four times as wide as the stem, bifid to one half the length, sinus obtuse, the lobes wide, somewhat divergent tapering to a single cell at the tip.

Perianth terminating a short lateral, 1.5 mm long, 0.5 mm wide, succeeded by an innovation from the same branch. Ventral and lateral keels well-developed, extending to half the length of the perianth. The upper parts of the keels are crested (Fig. 1D) and sometimes minutely papillose. The crests in Carr & Carr 1562, in which the perianth terminates a main stem followed by an innovation which also bears perianths, extend to half the length of the perianth. The crests are readily seen on the dry specimen, forming a structure like a minute biretta crowning the perianth. Perichaetial bracts 0.6 mm long, tips obtuse-acute, bracteole shortly bifid with acute lobes, 400 μm wide, 400 μm long.

Elaters of capsule, twisted, colourless, devoid of inner spirals, 170 μm long, Spores oval, 25 μm long, extine punctate.

Antheridial branch very short, with a very thin, fragile stem and therefore easily detached, and often lost when preparing specimens for microscopy; perichaetial leaves cup-shaped, 4-6 per branch.

Comment. Since it occurs often as a minor component of epicortical bryophyte consociations, this species must be the commonest of all the Lejeuneas of Victoria, contrary to Scott (1985) who reserves that epithet for *L drummondii .(*Also very common is *Harpalejeunea laetitans).* The vigorous plants of Carr & Carr 1562 had many perianths, often 4-6 per stem (Fig. 3E). The crested keels resemble closely those depicted by McVicar (1926: 430). Plants with large underleaves, larger than the postical lobe,were included by Lindbergh in his species *L planiuscula* (Lindb.)Buch. =*L. lamacerina.auct. plur.* but *planiuscula* differs from *cavifolia* in having composite oil bodies which disappear quickly after collection. Our specmens have large underleaves but numerous single but persistent oil bodies. They must therefore be retained in *L cavifolia.*

(3) Microlejeunea primordialis (Tayl.) St.

In Scott (1985) as *Lejeunea primordialis Gottsche.*
The following description is based on a specimen (5571) collected by Mrs Carr and myself in May 1957 growing on trees near Mason's Creek Falls, at Kinglake National Park, Victoria, in dense dark-green patches on tree bark together with other bryophytes.

Plants 15 mm long by 7 mm wide, glistening when dry (cf. *L. flava*) Leaves ovate, 135 μm long by 95 μm wide, imbricate, (Fig. 5A) overlapping the stem in antical view, bordered by two or three cell rows parallel to the leaf edge. The cells of the outermost row small, 15 μm wide, cells increasing in size away from the edge to 25 μm near the base (Fig. 5E). Cells with trigones and thickenings to the mid-walls. Oil bodies colourless, small, 10-20 per cell,

rod-shaped, fusiform or vermiform.

Postical lobes 175 µm long, 120 µm wide, inflated, the keel strongly curved, the free margin involute except near the apex where the free edge curves sharply to meet the basipetal edge of the antical lobe in a deep sinus. There is a single blunt tooth, consisting of one or two cells about midway along the free edge. Underleaves relatively large with a semicordate base, oval, 300 µm wide 220 µm long, bifid, the sinus narrow at about one third to one half the length, the lobes not divergent, obtuse at the base but ending in an acute tip. Stem 90 µm wide, of three rows of cortical cells in antical view (Fig. 6B). In section, (Fig. 6B) the stem shows three rows of medullary cells, as large as or almost as large as, the cortical cells an important feature of the subgenus *Microlejeunea* (Schuster, 1962:1). Antheridial branches sometimes paired, very short, with 6 bowl -shaped bracts, antheridia about 6.

Perianth terminal on a short branch (Fig. 5A), with an innovation from the main stem, 0.9 mm long by 0.4 mm wide, the beak 45 µm long. The keels strongly developed, crested near the apex, there somewhat papillose. Perichaetial bracts less than half the length of the perichaetium, bracteole oval, very shortly bifid. Capsule with a very short seta, elaters colourless with a vestigial internal spiral, spores not seen.

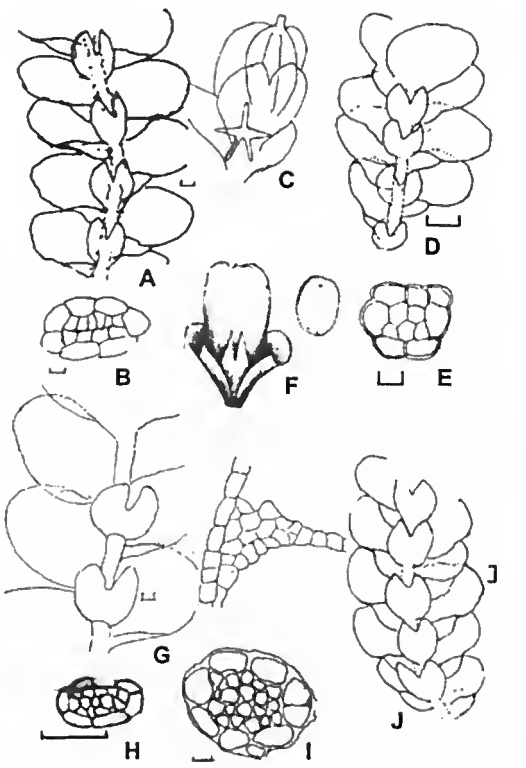


Fig 2. A-C. *L.tasmanica*. A, part of shoot. B, stem section. C, perianth, b=bract, k=large flattened keel. Arrow = cross section of perianth. D-F, *L.tumida* D, part of shoot. E, cross section of stem. F, perianth and its cross section (from Bastow, 1887) (Note the presence of a small beak but no keels). G-I, *L. subelobata*. G, part of shoot. H, cross section of stem. I, proximal part of lobule showing position of the tooth on lobule. J-K. *L.fawcettiae*. J, part of shoot. K, cross section of stem
Scale bars, D, 100µm. E, 10µm. F-K, 100 µm.

Comment. Scott (1985) chose to follow Gottsche in reducing this species fom *Microlejeunea* to *Lejeunea*. I now propose its reinstatment in an *Uuutaufung* (re-baptism) to use a term which has been used before in the bryological literature, having provided as full a description as I am able instead of Scott's (*loc. cit.*: 237) merely "a minute version of *L drummondii*". It is a much larger plant than that described by Scott ("0.5mm wide"). Arguments for retaining the sub-genus *Microlejeunea* are canvassed in a previous manuscript (Carr 2002) in describing a new species. According to Schuster (1963: 248) the species redescribed by Stephani (1912-1917) from material from "Aucklands Islands. New Zealand", is identical with *M. aucklandica* St. from the same locality. The illustrations in his unpublished *Icones* show one aberrant plant (called by him "*forma etiolata*") which differs considerably from those of the perhaps better developed Australian material (Fig. 6A). The leaves are shown as remote from each other on the stem, not overlapping (although in addition one, presumably "normal" stem is shown with overlapping, imbricate leaves). Microphyllous stems with remote leaves can be found in Australian specimens but they are atypical. The underleaves drawn by Stephani differ from those here described, but he does show one which has a sub-cordate base. The tooth on the lobule agrees (Fig. 6C), but not the papulosity of its keel (*fide* Stephani), and so do the strong keels of the perianth and the perichaetal bracts and bracteole, but he does not show the crests of the keels. His description (and illustration) has *M. primordialis* with smaller cells than described here, without trigones and without wall thickenings but *M. aucklandica* with relatively large trigones, Clearly the matter requires a critical comparison of material from both New Zealand and Australia for a complete resolution.

(4). *Lejeunea tnuida*, Mitten *in* Hooker *Journal of the Antarct. Voyage vol 2.*

Flora Nov Zel. 2, 157. Pl. CIII.

Schuster (1963: 249-251) has suggested using this species to typify a new subgenus, *Sphaerocolea* and provides not only a brief Latin protologue but a full description in English. He deseribes it as a "small, but rather variable speeies". The following description is of a speeimen (Carr and Carr 5572) eollected by Mrs Carr and myself in April 1957 growing on trees at a gully at Delley's Dell, The Grampians, Victoria. It has been matehed with a NSW speeimen determined by Stephani in *Herb.E Levier.*

Small delieate plants growing among other bryophytes, espeeially *Papillaria* sp. and *Metzgeria* sp.on the bark of trees. In small, yellowish-green patches, stems 10mm. long often in parallel groups ("fastigiate" - Sehuster's term *loc. cit.*) (Fig. 6F), irregularly branehed, the braneh es widely spreading. Leaves not remote, eontiguous to somewhat imbrieate, subereet to obliquely spreading or patent. The stem in eross seetion has 7 rows of eotical eells and 5-6 rows of medullary eells.(Fig. 2E). Leaves asymmetrie (Fig. 2D), ovate-faleate, eoncave towards the stem, 125 µm long 75 µm wide, in antieal view only just overlapping the stem whieh is 60 µm wide, leaf eells 21-25 µm diameter, (Fig. 4D) roughly polygonal with thin eell walls and very small trigones. Leaf bordered by a single row of smaller eells 18µm wide, leaves without oeelli. The leaf apex rounded, obtuse. Oil bodies very small, eolourless, oval or round. The leaves of the NSW speeimen are smaller, 100 x 75 µm . [The leaves of the speeimens (from North Island, New Zealand) deseribed by Sehuster (1963) were as large as 875µm long!] and the eells of the leaf eentre smaller, only 9um wide with fewer oil bodies than the Victorian speeimen. Nevertheless, both have eells which are unusual in shape - irregular reetangles or polygons (+ or - hexagons. *fide* Sehuster *loc. cit.*), thiekened at the angles ("eollenehymatous" *fide* Sehuster) almost the same in length as in width. Postieal lobe very inflated, half as long as the antieal lobe, 175 µm wide the free margin strongly involute except near the apex, keel very strongly convex, at the apex ending in a long, deep sinus as it joins the basipetal edge of the antieal lobe. The eoncavity of the antical lobe eauses a twist in the leaf where it meets the oppositely inflated lobule at its apex; a one or two-celled hyaline tooth (always two-eelled in Schuster's specimens) projeets from the free edge of the lobule near the apex. Sometimes the tooth eell is narrow and resembles a finger. Underleaves quite round, 325 µm x 325 µm [in Sehuster' s specimens, relatively small, and somewhat oval (160-210 x 165-180 µm) 62 x 55 µm in the NSW speeimen] i.e. four to four and a half times the width of the stem, bilobed, sinus rounded, situated at at about one half the length, lobes about eight eells wide at the base, tapering gradually to one or two eells at the aeute tip. Rhizoids frequent. The NSW speeimen has numerous diseoid gemmae, borne in the postieal lobes of the younger leaves; the Victorian specimen has them. also but only on the older parts of the plant (Fig. 3B) (the Schuster speeimens from New Zealand laeked gemmae). The stem seetion shows eight eortieal eell rows and 10 rows of smaller medullary eells.

Fertile perianth terminating a short lateral braneh (Fig. 3C), with an innovation from the same braneh, 0.6 mm long, 0.4 mm wide, elavate, fig-shaped, apex rounded, with a short beak and without keels (Fig. 2F).The NSW speeimen appears to have very short, small aeropetal keels but this may be an artefaet of drying. Periehaetial braets mueh shorter than the periehaetium, oval-aeute. The braeteole, 1.4 mm x 1.1 mm, i.e. more than three times as large as the underleaves.

Elaters of capsule eolourless, without an internal spiral, tips expanded (Fig. 5C). Spores oval, elongate through pregermination division. Extine punctate.

Antheridial braneh lateral, short, with 6 bowl-shaped braeteoles and 3 - 4 antheridia. The delieate leaves readily erode when old, the fragments possibly serving as vegetative propagules.

Comments. Sehuster (1963: 251) states that this speeies is perhaps "allied to theplant described by Stephani (1914-19) as *Lejeunea globosiflora* from Chile "whieh judging from Stephani's diagnosis is even smaller". I propose to draw attention to the fact that the rare Seottish species, *L. mevicari* Pearson, which oeeurs only in one loeality in western Seotland is perhaps identieal with *L. tumida.* The deseriptions of the two speeies given in Stephani (1914-18 Vol 5) are quite misleading. *L. tumida* is said to have a "5-plieate perianth with the postieal keels narrow but deeurrent, the antical keel strong but short". His drawing of a eross seetion of the perianth shows five prominent keels, whieh is at varianee with all other authors. *L. mevicari* is deseribed as "having no keels, but a strong beak". The perianths developed in *L. tumida* are of two kinds; the first infertile, has teminal lobes whieh are rounded, separate and entire and do not form a beak (Fig. 3A). The seeond kind, whieh is fertile, has five terminal lobes whieh eaeh produce a

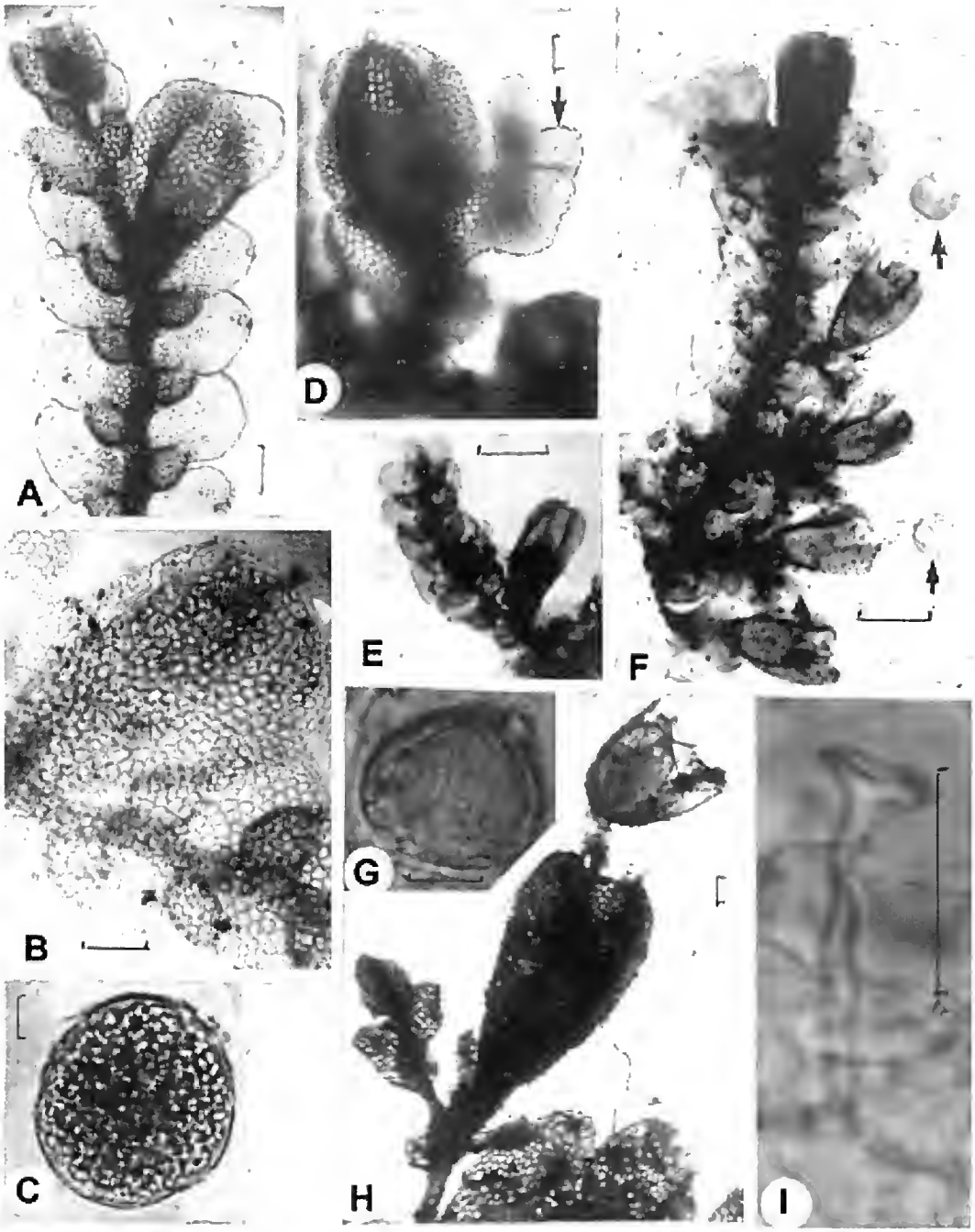


Fig. 3. Reproductive structures. A-C, *L. tumida*, A, pseudo-perianth (beakless) B, fertile perianth (arrow=beak). C, Gemma; D. *L. tasmanica*, Perianth with innovation (arrow). E-G, I, *L. fawcettiae*. E, perianth. F, shoot, terminated by perianth and with four seriate perianths terminating laterals, two of which have mature capsules (arrows). G, spore. I, elater. H, *L. subelobata*, perianth with innovation (In)
Scale bar=100μm
Scale bars. A - F = 100μm, G = 10 μm, I = 100μm.

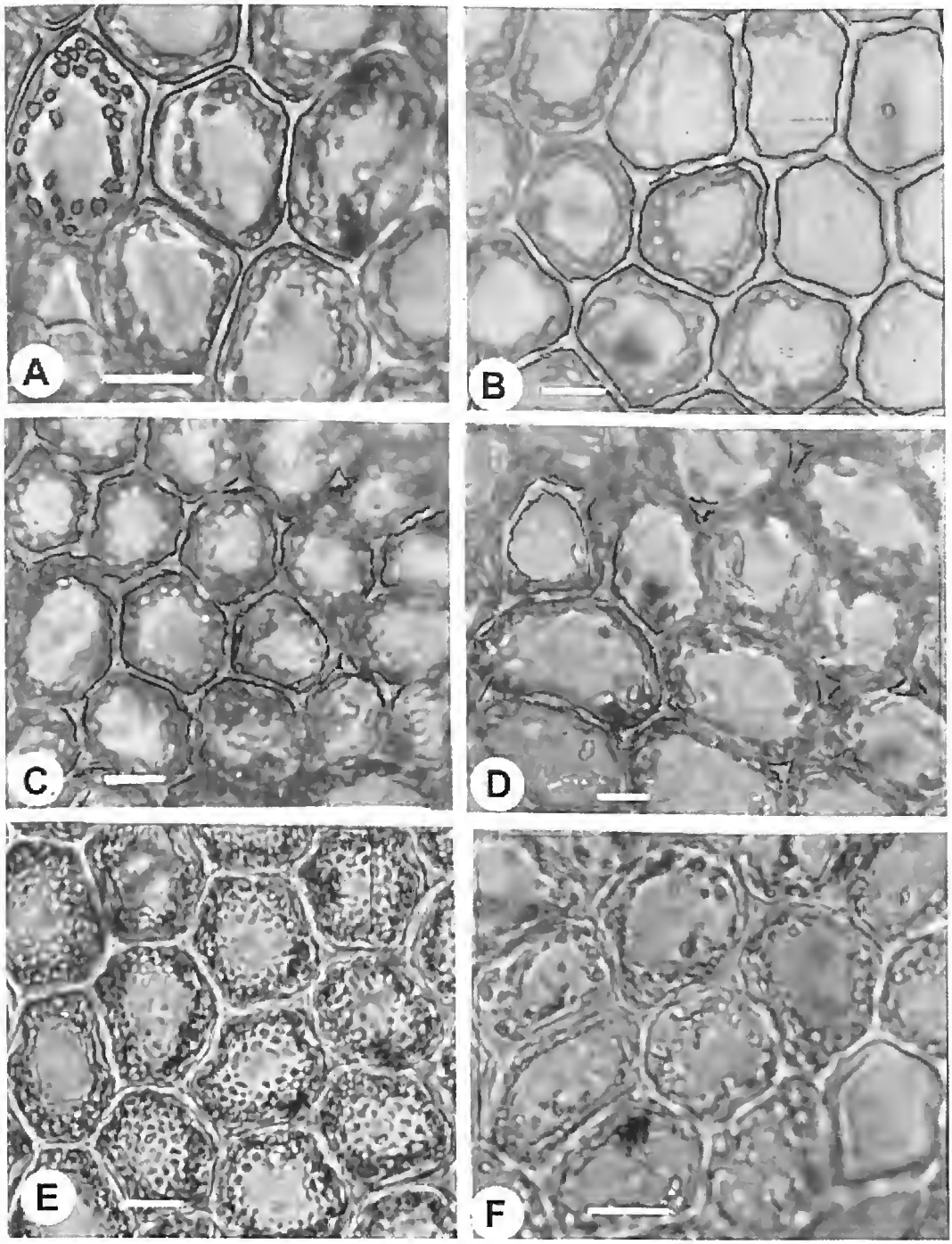


Fig. 4. Cells of the centre of the leaf. A. *L. flava*. B. *L. cavifolia*. C. *L. tasmanica*. D. *L. tumida*. E. *L. subelobata*. F. *L.fawcettiae*. Each scale bar 10μm

central, emergent set of cells, which conjoin with those of the other lobes to form a short beak (Fig. 3B) (Schuster's specimen had a "long slender beak" but no keels). The lobes are free only to about a quarter of their length. Both kinds of perianth were present on both the NSW and the Victorian specimens. The infertile, perianths or pseudo-perianths are referred to as "tube organs" by Goebel (1915-18,Vol 2:717). Goebel (*loc.cit.*: 718) records the same phenomenon in other liverworts (e.g.*Physotium giganteum*). The infertile perianth ("pseudo-perianth") is not followed by the production of an innovation. Since the beak is the product of apical meristem activity which fades soon after leaf intiation (Bopp & Feger, 1961) , the formation of the beak on the perianth lobes (leaf equivalents) is probably contemporaneous with the initiation of the archegonium at the stem apex. This explains why the pseudo-perianth lacks both beak and arche-gonium.

The description of *L. mcvicari* in McVicar (1924) agrees in all major particulars with that of *L. tumida* although infertile perianths and gemmae are not mentioned, perhaps through lack of intensive study of this very rare species. Rodway (1916) clearly describes and illustrates the keel-less nature of the perianth in *L tumida*. Clearly the species is very variable and deserves further study over its whole range in the same way that was done by Schuster (1962) for *Microlejeunea ulicina*. In all probability, in my opinion, the species, which is widespread in Tasmania, has been spread by the unwitting activity of man to a site in Inverness. The comparatively late (1900) discovery of *L. mcvicari* is in agreement, together with the remarkable apparent identity of the two species. Schuster (1983: 612-3) refers to the inadvertent and successful introduction of antipodal bryophytes to Britain, for instance, the moss "*Orthotrichum lineare Schwaegr.* which was introduced, apparently fom the Southern Hemisphere where it is indigenous, to the Liverpool district around 1911 and rapidly spread throughout Britain". Similarly he continues, "*Campylopus introflexus*, indigenous to the Southern Hemisphere has been introduced into Western Europe and since 1941, has spread explosively throughout the British Isles ..... Subsequent to their introduction these species have been confused with species native to Britain or Europe". These mosses are much more aggressive colonists than *L tumida* which if it is indeed identical with *L. mcvicari* does not seem to have spread from its original Scottish locality following discovery.

Another species which could well be placed in *Sphaerocolea* is the New Zealand *Taxilejeunea colensoana* St., which Schuster (1963: 251) suggests should be placed in *Lejeunea s. lat.* and (Schuster 1963: 250) regards as a synonym of *L. tumida*. It has the massively inflated lobules and keelless perianths of the other two species. Schuster perhaps wrongly accuses Stepheni (*loc. cit.*: 250) of placing *tumida* in *Taxilejeunea*. It is true that *colensoana* was tentatively placed there by Stephani, "on the basis of the diffuse gynoecia".

Scott's (1985) only comment on *L. tumida* is to the effect that the (presumbly Victorian) records of it "are probably mostly *L. drummondii*". If this is correct it is a sad reflection on the abilities of previous hepatieologists of Victoria.

(5). *Lejeunea subelobata* Carr & Pears. 1887. Linn. Soc NSW, 1439.

The following description is based on a specimen (Carr and Carr 3571) collected by Mrs Carr and myself, March 1957. It was growing on a rock at water level in the Tooronga River near Noojee, Victoria. Another specimen (not numbered and now lost) was epiphytic on a moss, *Weymouthia cochearifolia* in a fern gully at Kallista. They have been compared with specimens fom NSW, verified by Stephani. The NSW specimens are frequently mixed with another elobulate *Lejeunea* which appears to be *L. aloba* St. (Stephani, 1918, Vol 5: 767) from New Caledonia, which differs in the much smaller numbers of oil bodies per cell and in the much narrower underleaves with divergent, lanceolate lobes. The Victorian specimens do not have this admixture.

Plants growing in dense patches on wet rocks , pale green, stems to 10mm long, irregularly branched. Leaves closely imbricate, patent , somewhat concave, broadly ovate or spathulate (Fig. 2G), the apex rounded, the base narrowed to the median, 0.7mm. long x 0.5mm max.width, with a sloping and relatively narrow attachment to the stem, in antical view the aeropetal edge not crossing the stem. Despite its relatively wide oval shape the leaf is attached quite narrowly to the outermost merones of the stem both dorsally and ventrally. Postical lobe very small or absent,when well developed 200µm. long x 70µm. wide, with a blunt tooth near the apex (Fig. 2G). Cells of centre of leaf 20µm. in diameter, (Fig. 4E) roughly hexagonal with very small trigones, cell walls dark - coloured, uniformly thickened, minus mid-wall thickenings. Oil bodies minute, dark coloured , oval,

very numerous, 25-45 per cell, almost filling the lumen, so that the leaf lacks transluceney (Fig. 4E). Cortieal eells of stem 32 µm wide, with about 8 eortical cells, medullary eells narrower in five to six rows (Fig. 211). Underleaves large, about two and a half to three times the stem width, round or oval, with a subeordate base, diameter 350µm, sinus about one fifth the depth, obtuse, the wide lobes not divergent, rounded at the tips. The stem seetion shows 8 rows of cortieal eells and ten rows of relatively thick-walled medullary cells. Perianth terminating a lateral braneh with a subsequent innovation from the main stem (Fig. 3G), small, pyriform, 0.5mm long, x 0.25mm wide, with a relatively long beak, 88µm long. Keels of perianth extending to the full length. Periehaetial braets about half as long as the periehaetium, braeteole oval, bifid, the lobes laneeolate. Capsule (Fig. 1 ,8) with a fairly long, jointed seta, emerging at least 250 µm from the perianth, elaters about 200µm long, without an inner spiral, tips not inflated. Spores 11-12µm long, oval, extine minutely punctate.

Antheridia often in pairs on oppoaite sides of the stem, eaeh on a very short branch, with two-three pairs of bracts.

(6) *L. tasmanica*. Gottsche, Linnea, 1856.

This species is common in Tasmania and is also widespread in NSW.

The following deseription is based on a speeimen (Carr & Carr 1563) eollected by Mrs Carr and me, January 1956 from the bark of the ultimate braneh es of a small tree at Tom Tregellen's gully, Kallista, Victoria, and another, (Carr & Carr 4570), colleeted April 1957 on the floor of the fern gully at Delley's Dell, near Hall's Gap, the Grampians, Vietoria with other bryophytes (*Bazzania sp.* and mosses).

Creeping, elosely adpressed to the bark of smooth-barked trees, mixed with *Radula buccinifera* or admixed with other bryophytes in moist, eool situations. Mid green, stems to 20 mm length, irregularly braneh ed. Leaves elosely imbrieate, ovate elliptical, 0.6mm by 0.4mm, spreading at an angle of between 90 and 60 degrees to the stem (Fig. 2A). Cells of the eentre of the leaf 37.5µm (Fig. 5C), cells bordering the margin 14 µm wide. There are four to five longitudinal rows of cells parallel to eaeh of the margins of the leaf (Fig. 5B).

Cell walls uniformly thin without thickenings or trigones. Oil bodies homogeneous colourless, minute, spherical to bacilliform, 4-10 per eell. Underleaves three times as wide as the stem, round, 0.2mm diameter, base subcordate, divided to half the length, sinus narrow, aeute, lobes eonvergent, apieulate terminating in one or two eells. The underleaves increase in size acropetally, from 0.15mm diameter at the base of the stem.

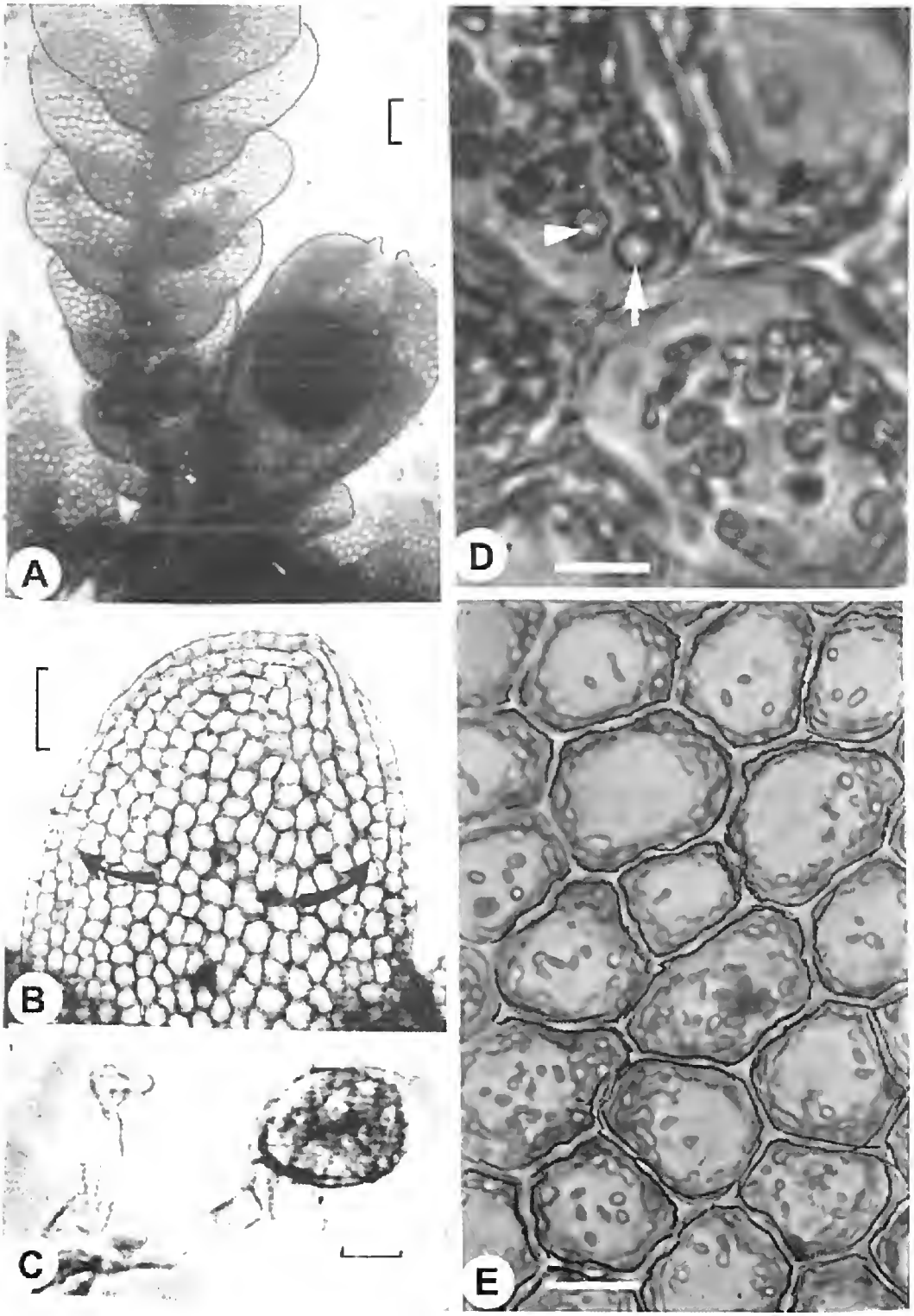
Postical lobe large, inflated, 125 µm long, 65 µm wide the free edge somewhat involute the one, or more usually, two-eelled tooth very elose to the apex turned towards the stem. The stem has the seven rows of eortieal eells as is usual for *Lejeunea* speeies and about ten medullary cell rows (Fig. 2B).

Perianth terminating a short lateral followed by an innovation from the same braneh (Fig. 3D) with four large braets, eaeh rounded at the tip and extending about three-quarters the length of the perianth, braeteole bifid, 210µm long. Perianth 0.9mm long by 0.4mm wide with a short but well-marked beak and five prominent, strongly flattened keels whieh extend almost the full length (Fig. 2C). Antheridial braneh a very short lateral with six bracts.

Comments. The regularity of the eellular construetion of its leaves, eonsisting of a single row of narrow eells forming a border, inside which are nested four or five regular ellipses of larger eells, with the eentre of the leaf eonsisting of almost linear rows of the largest cells running from the base towards the apex (Fig. 5B), is so unusual as to deserve an adjective: *campylocytic* analogous to the term for a similar type of Angiosperm leaf venation (see Carr, 2003). This feature, eoupled with the absence of eell wall thiekenings or trigones, the large mid-leaf cells and the small number of minute colourless oil bodies are features sufficiently distinetive as to make specimens of *L. tasmanica* easily distinguishable at a glanee from all other Victorian *Lejeuneas* with oval leaves and round bifid underleaves. This and the distinetive features of the perianth with its large, wide flattened keels and large bracts and braeteole make this an easily identified species. The speeimen described differs from that of the original deseription only in its smaller leaves and the antheridial braneh having six rather than only one to two braets.

(7) Lejeunea fawcettiae. D.J.Carr. *sp nov.*

Holotype. The following deseription is based on the speeimen (Carr, S.G.M. 357) colleeted by Mrs Carr


A
B
C
D
E

in March 1957 growing on the bark of a blackwood (*Acacia melanoxyon*) tree near the Railway Station, Tooronga Falls, Noojee, Victoria.

Another specimen was collected by both of us Jan. 1956 (Carr & Carr 1560) on tree branches in the Otways, Victoria.

In cortice cespitans alliis hepaticis consociata, pallide griseo-viridis, folia caulis contigua, valde concava symmetrica. Lobulus majuscula inflata. Amphigastria caulina majuscula ad caule quinque latiora, subrotunda ad 1/4 inciso biloba sinus recto. Perianthia in ramulo parvo terminalia repetitas (x5) *seriata. Androecia sessilis, seriata.*

In pale grey-green patches appressed to the substratum. Stems to 5mm long, branched, somewhat pinnately near the base of the stem, forming autoicous plants about 2 - 3mm wide. Leaves closely imbricate, concave, oval, 0.6mm long, 0.3mm wide, apex rounded, incurved, subobtuse (Fig. 2J). Cells of centre of leaf 35µm wide, roughly hexagonal (Fig. 4F). leaf bordered by a single row of cells each 15 µm wide. Cell walls thin, with small trigones and occasional small mid cell-wall thickenings. Oil bodies10-30 per cell, minute, oval to polygonal (irregularly 5-6 sides), each oil body with a refractive spherical inclusion (Fig. 5D). Postical lobes strongly inflated 375 µm long x 345 µm wide. Keel strongly curved, terminating at the apex in a deep sinus where it meets the antical lobe, free edge more-or-less involute. Underleaves large, round or oval 0.5 mm in diameter. (i.e. up to five times as wide as the stem) with a narrow sinus and not divergent lobes. Stem 100µm wide Stem section shows 12 rows of cortical cells and 24 medullary rows (Fig. 2J).

Perianths small (each 0.4 mm. x 0.2 mm) commonly borne in series on short branches (Figs 3E-F) on the lower part of the stem, each terminating a lateral branch Occasionally a perianth terrminates a main shoot (Fig. 3F). Keels strongly developed to about half way. Beak prominent, 20 µm long.

Antheridial branches lateral, short often several seriate on a single stem, (cf. perianths) (Fig. 6G) bracts rounded.

Elaters colourless, 150 µm long, (Fig. 3I) without an internal spiral; tips expanded.

Spores bluntly triangular or cardioid (Fig. 3G) due to precocious pregermination divisions, the extine covered with punctiform emergences arranged in a curvilinear pattern.

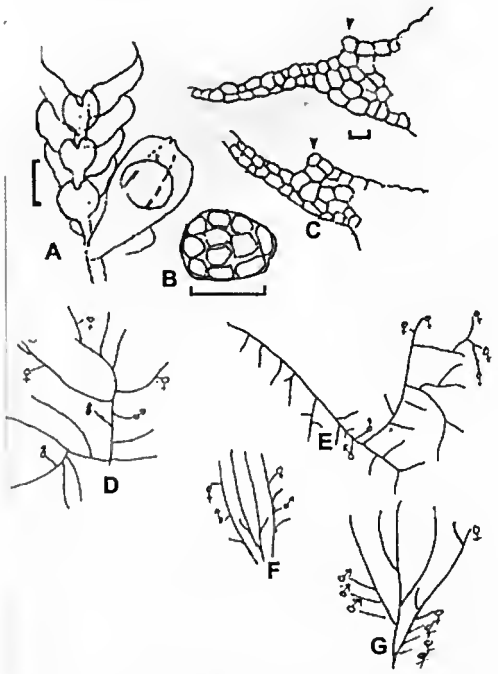


Fig 6. A-D. *Microlejeunea primordialis.* A. Part of shoot with perianth. B, cross section of stem. C, lobules with teeth (arrows). D, Growth habit (schematic) Scale bars. A & B, 100µm, C, 10 µm. E-G. Growth habits of species of *Lejeunea* (schematic). E, *L cavifolia* (from Carr & Carr, specimen 1562). F, *L. tumida.* G. *L. fawcettiae*

Comment. The species is named for its discoverer, my wife née S.G.M.Fawcett. Were the taxon *Taxilejeunea* to be resuscitated, perhaps as as a subgenus of *Lejeunea,* following its suppression by Schuster (1963), for species with large bifid underleaves and seriate perianths, *L. fawcettiae* would be a candidate for inclusion in it.

ACKNOWLEDGMENTS

I am indebted to Professor B.E.S. Gunning, FRS. FAA., of RSBS, ANU, for encouragement and for arranging for cross-sections to be made of the stems of the specimens, and to Dr Sally Stowe, Electron Microscopy Unit, RSBS, for having these made. I also wish to thank Mrs Janette Lenz, Mrs Anne Catling and Mr. Roland Jahnke for their support and encouragement, as well as my former colleagues.

Fig. 5. Miscellany. A.& E. *Microlejunea primordialis.* A. Perianth . Scale bar = 100µm B. *L. tasmanica.* campylocytic leaf. Arrows, several rows of longitudinal rows of cells, Scale bar = 100 µm. C. *L tumida.* Spore and elaters , Scale bar = 10µm. D. *L fawcettiae.* Heterogeneous oil bodies with inclusions (arrows), Scale bar = 10µm E. *M. primordialis,* cells of centre of leaf. Scale bar=10µm.

Professors Martin Canny, Margaret McCully and Adrian Gibbs for generous support and for supplies of materials for microscopy. Thanks are also due to Dr J. H. Ross, Chief Botanist, National Herbarium, Victoria for information supplied.

REFERENCES

Bastow, R.A., 1887. Tasmanian hepaticae. *Papers and Proceedings of the Royal Society of Tasmania 1887:* 209-234. 35 plates.

Bopp, M. & Feger, F., 1961. Das Grundschema der Blattentwicklung bei Leber-moosen. *Revue de bryologie et lichenologie* 29: 256-273.

Carr, D.J, in press. Two new bryophytes endemic to Victoria. Submitted to *Proceedings of the Royal Socety of Victoria.*

Carr, D.J, in press. Cell patterning in leaves of *Lejeunea* species (Hepaticae), Submitted to *Phytomorphology.*

Goebel, K., 1915-18. *Organographie der Pflanzen.* Vol 2. *Spezielle Organographie. Archegoniatae.* Jena. G Fischer.

McVicar, S.M. *Student's handbook of British Hepatics*, 2nd Edition. Wheldon & Wesley, London.

Mizutani, M., 1962. A revision of Japanese Lejeuneaceae. *Journal of the Hattori Botanical Laboratory*, 24: 115- 302, Figs 1-39.

Richards, P.W., 1984. The ecology of tropical forest bryophytes. Chapter 21. In *New Manual of Bryology*, vol 2. R.M. Schuster, ed., Hattori Botanical Laboratory, Miazawa, Japan. 1233-1270.

Rodway, L., 1916. Tasmanian Bryophytes.Vol 2, Hepatics. *Papers and Proceedings Royal Society of Tasmania* Hobart.

Schuster, R.M., 1962. North American Lejeuneaceae VIII. *Lejeunea* subgenera *Microlejeunea* and *Chaetolejeunea. Journal Hattori Botanical Laboratory*, 25: 1-80.

Schuster, R.M., 1963. Studies in Antipodal hepaticae I. Annotated keys to the genera of antipodal hepaticae with special reference to Tasmania and New Zealand. *Journal Hattori Botanical Laboratory*, 26: 185-309.

Schuster, R.M., 1983. Phytogeography of the Bryophyta. Ch 10. In *New Manual of Bryology* Vol. 1. R.M. Schuster, ed., Hattori Botanical Laboratory, Miazawa, Japan, 463-626.

Scott, G.A.M., 1985. *Southern Australian Liverworts.* Australian Flora and Fauna Series No 2. Australian Government Publishing Service, Canberra.

Stephani, F., 1914-1917 *Species Hepat-icarum,* 7 vols., Georg & Co., Geneva & Basel.

Stephani, F. & Watts, W.W., 1914. Hepaticae Australes. *Journal and Proceedings of the Royal Society of New South Wales,* 48: 94-135.

Manuscript received 8 June 2003
Manuscript accepted 7 December 2003

DESCRIPTION OF *LOXOCYTHERE (NOVOLOXOCYTHERE) PELIUS* SUBGEN. *ET* SP. NOV. (OSTRACODA) FROM THE CENOZOIC OF S.E. AUSTRALIA WITH COMMENTS ON SPECIES OF *ANTARCTILOXOCONCHA* HARTMANN, 1986 AND *LOXORETICULATUM* BENSON, 1964 FROM AUSTRALIAN AND ANTARCTIC MARINE WATERS

MARK THOMAS WARNE

School of Ecology and Environment, Deakin University (Melbourne Campus), 221 Burwood Highway, Burwood, Victoria 3125, Australia.

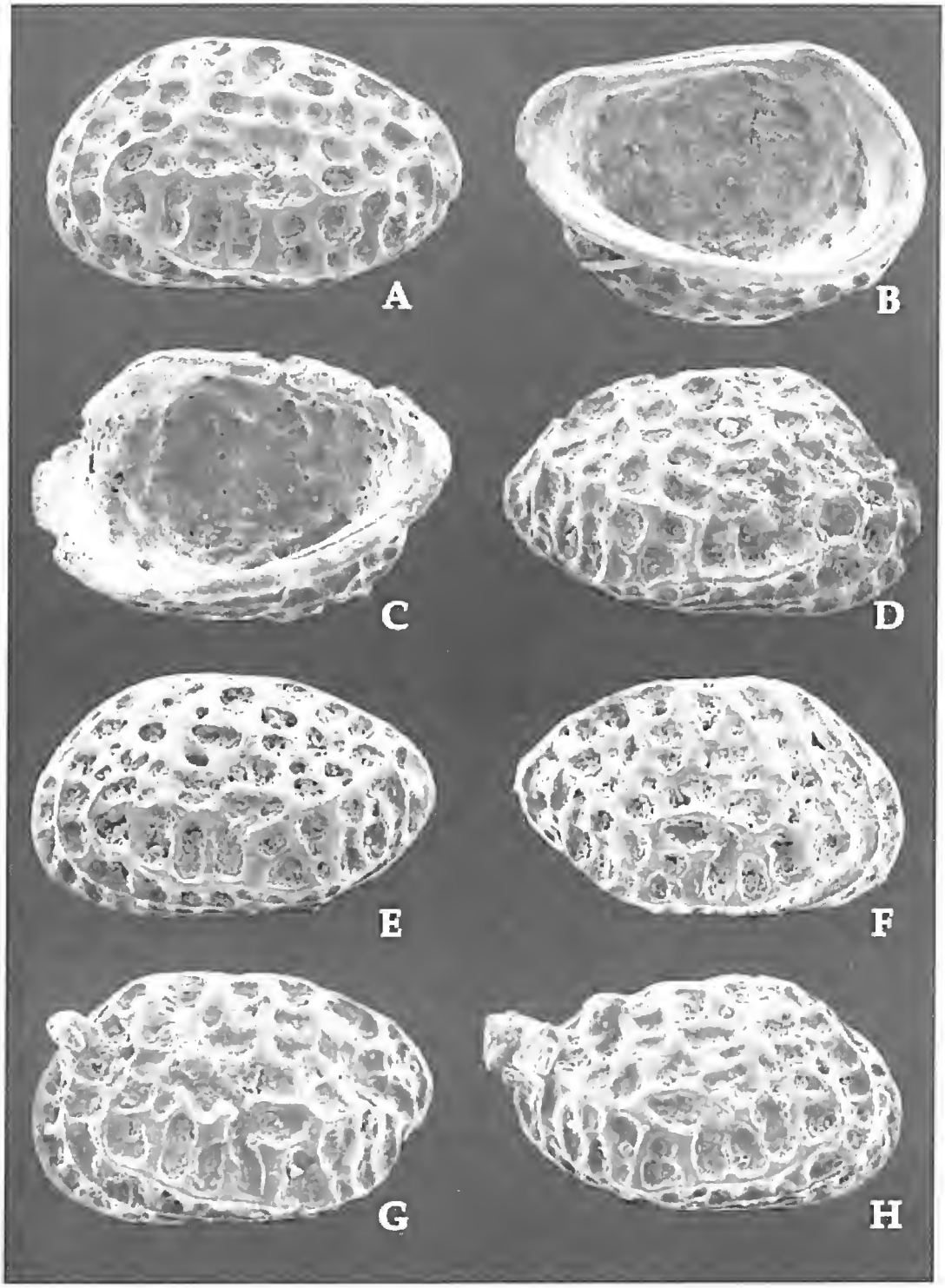
WARNE, M.T., 2004:12:04. Description of *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov. (Ostracoda) from the Cenozoic of S.E. Australia with comments on species of *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 from Australian and Antarctic marine waters. *Proceedings of the Royal Society of Victoria* 116(2): 233-241. ISSN 0035-9211.

Loxocythere (Novoloxocythere) pelius subgen. *et* sp. nov. is described from Upper Miocene strata of the Port Phillip and Western Port Basins, Victoria. It has its acme in shallow open marine facies of latest Miocene (Cheltenhamian) age. This species, along with *Loxocythere (Novoloxocythere) kerryswansoni* Yassini and Jones, 1995, forms a discrete group of rotund Australian *Loxocythere* species that possess posterior extremities in both valves that are positioned well above mid carapace height (i.e. adjacent to dorsal margin). This feature along with a sub-triangular inner margin outline, defines a carapace shape that is distinct from that of rotund species of *Loxocythere (loxocythere)* Hornibrook, 1952 and *Antarctiloxoconcha* Hartmann, 1986. The type species of *Antarctiloxoconcha* - *A. frigida* (Neale,1967), possesses internal carapace features that are very similar to the type species of *Loxocythere* - *L. crassa* Hornibrook, 1952. Both have relatively short carapaces and sub-quadrate inner margin outlines with posterior extremities in both valves positioned below mid carapace height. Species of *Loxocythere (Novoloxocythere)*, in particular *L. (N.) kerryswansoni*, have a carapace shape that is transitional between *Loxocythere* and *Loxoreticulatum* Benson, 1964. Species of *Loxoreticulatum* generally possess a sub-parallelogram shaped carapace / inner margin and arched median hinge element. The latter feature is distinct from the mostly straight median hinge elements of *Loxocythere (Loxocythere)* and *Loxocythere (Novoloxocythere)* species. Species of *Loxocythere (Novoloxocythere)* are also readily distinguishable from relatively elongate species of *Loxocythere*, such as *L.(L.) hornibrooki* McKenzie, 1967, as the latter possess long (for genus), sub-rectangular shaped carapaces / inner margin outlines and posterior extremities below mid height.

Key words: Ostracoda, *Loxocythere (Novoloxocythere) pileus*, *Antarctiloxoconcha*, *Loxoreticulatum*, Cenozoic, Australia, Antarctica

THE OSTRACOD genus *Loxocythere* Hornibrook, 1952 includes a number of different, morphologically discrete, species groups. Differentiation of these *Loxocythere* species groups can be achieved by analysis of overall carapace shape characteristics and valve inner margins outlines. The main aims of this paper are to describe one new species of *Loxocythere* present in Upper Miocene strata of S.E Australia and to outline the carapace attributes of different *Loxocythere* species groups, one of which is here designated as a new subgenus. The genera *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 are here also considered as species belonging to these two genera possess carapace characteristics that are very similar to those of some *Loxocythere* species.

The specimens of *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov. illustrated herein (Figs. 1 & 2) were collected from a sedimentary unit referred to as the Warneet Sands by Warne 1987, 1993. This formation occurs subsurface over a restricted geographical extent near the township of Warneet in the northwest of the Western Port Basin, S.E. Australia. The specific sediment sample from which the figured specimens were extracted was a calcareous and ferruginous sand of shallow marine origin occurring in the Geological Survey of Victoria borehole Sherwood


A
B
C
D
E
F
G
H

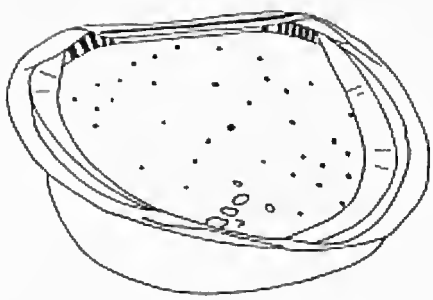


Fig. 2. *Loxocythere (Novoloxocythere) pelius* sp.nov.; line drawing, adult male, left valve, internal view, P122292, from type locality, magnification x 110

18 (38° 12'S, 145°16'E) between the intervals of 20m and 22m. The unit is probably latest Miocene being broadly equivalent in age to the basal "nodule bed" horizon of the Sandringham Sand in the Port Phillip Basin (Jenkins, 1962; Warne, 2002). The "Warneet Sands" disconformably overlie the Miocene Sherwood Formation of the Western Port Basin, and underlie Plioeene (?) non-marine sediments termed the Warneet Beds by Jenkins, 1962. It is here thought that the "Warneet Sands" / Warneet Beds sueeession of the Western Port Basin is similar to the Black Rock Sandstone / Red Bluff Sand (= Sandringham Sand) sueeession of the eastern Port Phillip Basin. *Loxocythere (Novoloxocythere) pelius* is quite eommon in both the basal units of these two suecessions and might be deseribed as having its acme in S.E. Australia during the early Cheltenhamian (see figure 3 in Warne 2002). Figured specimens of *L. (N.) pelius* are housed in Museum Victoria under the registration numbers P 122290 – P122293, P122295, P311645. Other specimens figured herein have the Museum Victoria registration numbers P311653, P312080, P312081.

COMPARATIVE MORPHOLOGY

In praetiee, and up until the present time, larger Australasian adult speeimens belonging to the broad *Loxocythere / Microcytherura* group of speeies have been placed in *Loxocythere,* and smaller adult speeimens have been placed in *Microcytherura* G. W. Müller, 1894. This is despite the observation of Hornibrook, 1952, who noted that there was marked differenee in (adult) earapaee size for *Loxocythere crassa* in different modern marine environments of New Zealand. This observation highlights the point that the genus *Loxocythere* can inelude both large and small speeies relative to the overall range in adult sizes within the *Loxocythere / Microcytherura* "taxonomie plexus". Further eomments on the relationship between the genera *Loxocythere* and *Microcytherura* are ineluded in Warne (2004).

Loxocythere (Loxocythere) Hornibrook, 1952

The *Loxocythere* type speeies *L. crassa* Hornibrook, 1952 is in part distinguished by its thiek shell, rugged retieulate ornament, subquadrate shaped inner margin and posterior extremity below mid height. This partieular eombination of eharaeters is seen in no other eurrently known speeies of *Loxocythere.* Other speeies here plaeed in *Loxocythere (Loxocythere)* fall into two morphological groups based on earapaee features. The first group ineludes speeies sueh as *L. kingi* Hornibrook, 1952 and *Loxocythere variasculpta* Whatley *et. al.*, 1997, which have relatively elongate subreetangular earapaees and inner margins, and acutely rounded posterior outlines with valve posterior extremities well below mid height (i.e. *L. kingi*; Fig 3 A-B). The seeond group ineludes speeies sueh as *L. hornibrooki* McKenzie, 1967 , *L. onyenensis* (Chapman, 1914) and *L. inflata* Hanai, 1959, which also have relatively elongate subreetangular earapaee and inner margin outlines, but differ from other groups of *Loxocythere (Loxocythere)* speeies by possessing broadly rounded posterior extremities. Further diseussion of this latter group of *Loxocythere* speeies is included in Warne (2004).

Loxocythere (Novoloxocythere) subgen. nov.

The known speeies within this subgenus are *Loxocythere (Novoloxocythere) pelius* sp.nov. and *Loxocythere (Novoloxocythere) kerryswansoni* Yassini and Jones, 1995. These speeies are distinguished by

Fig. 1. *Loxocythere (Novoloxocythere) pelius* sp. nov. All specimens from type locality (late Late Miocene). Magnification of all specimens x 118. A. Paratype, left valve, male, external view, P311645. B. Paratype, left valve, male, internal view, P311645. C. Holotype, right valve, female, internal view, P122293. D. Holotype, right valve, female, external view, P122293, E. Paratype, left valve, male, external view, P122292. F. Paratype, right valve, juvenile female?, external view, P122291. G. Paratype, left valve, juvenile female?, external view, P122290. H. Paratype, right valve juvenile female?, external view, P122295.

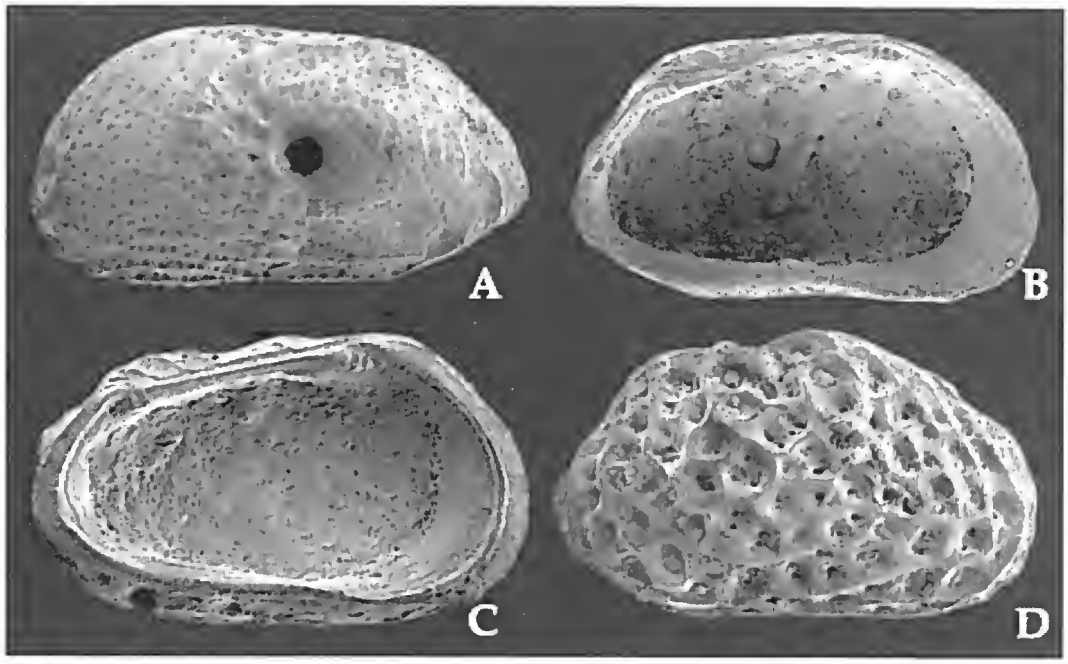


Fig. 3. A & B. *Loxocythere kingi* Hornibrook, 1952. Specimen from sea floor at 100 fathoms depth off Three Kings Island, New Zealand. A. External view of left valve (P311653), x 172. B. Internal view of left valve (P311653), x 172. C & D. *Loxocythere crassa* Hornibrook, 1952. Specimens from sea floor at 100 fathoms depth off Three Kings Island, New Zealand. C. Internal view of left valve (P312080), x 175. D. External view of right valve (P312081), x 174.

their subtriangular shaped inner margin and posterior extremity well above mid-height. This subgenus includes species (in particular *L. (N.) kerryswansoni*) that are transitional or convergent in morphology (carapace shape) towards *Loxoreticulatum*. *L. (N.) kerryswansoni* is known from shallow marine waters of south-east and north-east Australia. *L. (N.) pelius* is only known from fossil material. Current records indicate that this species inhabited Mio-Pliocene shallow marine environments of S.E. Australia.

Antarctiloxoconcha Hartmann, 1986

This group includes rotund species with subquadrate inner margins and posterior extremities well below mid height. Species belonging to this genus include *Antarctiloxoconcha frigida* (Neale, 1967) (type species), and possibly *Antarctiloxoconcha? malzi* (McKenzie, Reyment and Reyment, 1993) n. comb. *Antarctiloxoconcha? vermiculatum* (Whatley, *et. al.*, 1988) n. comb. *Antarctiloxoconcha? phascolus* (Neil, 2000) n. comb. and *Antarctiloxoconcha? burdwoodbankensis* (Whatley and Cusminsky, 2002) n. comb. (although a number of the latter four species may ultimately warrant separate subgeneric status). Hartmann, 1986 regarded the type species as belonging to the Loxoconchidae Sars while Neil, 2000 originally regarded the species *Antarctiloxoconcha? phascolus* as belonging to the family Eucytheridae Puri. Whatley *et. al.*, 1998 considered that the species *Antarctiloxoconcha frigida* to be a cytherurid placing it (with reservation) in the genus *Cytheropteron* Sars, and interestingly noted a possible affinity with the genus *Pelecocythere* Athersuch. Despite these diverse views, the interior margin shape, adductor muscle scars, and to a lesser extent, terminal hinge elements of the *Antarctiloxoconcha* type species *A. frigida* (see illustrations in Hartmann, 1989; plate 8, figs. 6 and 7), are very similar to the *Loxocythere* type species *L. crassa* (see Fig. 3C of this paper and Hartmann, 1982; plate 1, figs. 5 and 6). Hartmann, 1986 indicated that the soft part anatomy of the type species of *Antarctiloxoconcha* is consistent with the placement of this species in the Loxoconchidae. However, as noted by Athersuch and Horne, 1984, there is variance in opinions concerning the diagnosis of the family Loxoconchidae. As a consequence, and in spite of its name, the genus *Antarctiloxoconcha* it is here considered to have a close morphological relationship to some genera of the family Cytheridae Baird. This

broadly agrees with the original placement of *A. frigida* by Neale (1967) in the genus *Loxocythere*. Compared to the *Loxocythere* type species (*L. crossa* - Fig. 3 C-D), species of *Antarct-iloxoconcha* are more rotund in external shape, have more subdued external ornament and posses a strongly crenulated and slightly arched medium hinge element (see Hartmann, 1989; plate 8, figs 4-7). Species here included in *Antarctiloxoconcha* have or had a Southern Ocean (coastal Antarctica & southern Australia) or south-west Atlantic Ocean (continental shelf) distribution.

Loxoreticulatum Benson, 1964

This genus is distinguished by its sub-parallelogram shaped carapace and inner margin, lack of a strongly inflated venter and arched median hinge element. This combination of features is best developed in the type species *Loxoreticulatum fallax* G. W. Müller, 1908. Other species such as *Loxoreticulatum hempeli* Hartmann, 1987 possess a more subrectangular rather than sub-parallelogram shaped carapace, a *Loxocythere*-like inflated venter, a *Loxocythere*-like shaped inner margin and nearly straight median hinge elements. With respect to these carapace features, *Loxoreticulatum hempeli* is transitional towards species such a *Loxocythere (Novoloxocythere) kerryswansoni*. Since the taxon *Loxoreticulatum* includes forms that are transitional in carapace morphology towards some species of *Loxocythere*, it is here suggested that a relatively close taxonomic relationship exists between *Loxoreticulatum* and *Loxocythere*. This is despite the fact that G. W. Müller, 1908 (see Benson, 1964) noted that the soft part anatomy of *Loxoreticulotum* was *Cytheropteron*-like in character (see also Hartmann, 1987). Perhaps significantly, unlike the vast majority of species belonging to *Cytheropteron*, species of *Loxoreticulatum* lack a distinctly alate ventral region. Species of *Loxoreticulatum* have been recorded from shallow marine waters of coastal Antarctica and the south-west Atlantic region.

SYSTEMATIC PALAEONTOLOGY

Subclass Ostracoda Latreille, 1806
Order Podocopida G.W. Müller, 1894
Suborder Podocopina Sars, 1866
Superfamily Cytheracea Baird, 1850
Family Cytheridae Baird, 1850

Subfamily Cytherinae Baird, 1850

Genus **Loxocythere** Hornibrook, 1952
Subgenus **Novoloxocythere** subgen.nov.

Type species, *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov.

Etymology: *Novo* (= new) added as a prefix to *Loxocythere*. A reference to this being a new group of *Loxocythere* species.

Diagnosis: A group of *Loxocythere* species with very distinct sub-triangular shaped inner margins and posterior extremities well above mid height. Other features as for *Loxocythere s.s.*

Remarks: *Loxocythere (Loxocythere)* and *Antarctiloxoconcha* differ from this new subgenus in having subquadrate to subrectangular shaped inner margins and posterior extremities below mid height. *Loxoreticulatum* differs from *Loxocythere (Novoloxocythere)* in that the former has a sub-parallelogram shaped inner margin and gently arched medium hinge element. The sub-triangular shaped inner margin in species of *Loxocythere (Novoloxocythere)* is developed because of the presence of a very much shorter posterodorsal slope than occurs in *Loxocythere s.s.*. Two named species are currently recognised as belonging to this subgenus; *Loxocythere (Novoloxocythere) pelius* sp.nov. and *Loxocythere (Novoloxocythere) kerryswansoni* Yassini and Jones, 1995. Whilst *Loxocythere (Novoloxocythere) kerryswansoni* has an inner margin shape that is transitional towards that of some species of *Loxoreticulatum*, it lacks the arched median hinge element characteristic of *Loxoreticulatum* species.

Cytherurid species such as *Cytheropteron*? *infrequens* Mostafawi, 1992, *Oculocytheropteron macropunctatum* Whatley *et. al.*, 1988, *Oculocytheropteron micropunctatum* Whatley *et. al.*, 1988 and *Oculocytheropteron reticulopunctatum* Whatley *et. al.*, 1988, are also very similar in carapace shape to *L.(N.) kerryswansoni*, although can be distinguished by their arched (to varying degrees) LV dorsal margins and medium hinge elements, lower posterior extremities and distinctive (although subdued) *Cytheropteron*-like alate extensions. The close similarity in shape between *L. (N.) kerryswansoni* and species such as *Cytheropteron*? *infrequens*, is here considered to reflect convergent evolution in carapace morphology.

One other taxon, the cytheropterine *Heinzmalzia rhombiformis* (Chen) *sensu* Mostafawi, 1992 is superficially similar in external morphology to the type species of *Loxocythere (Novoloxocythere) - L.(N.) pelius*. However, *H. rhombiformis* has a very characteristic *Cytheropteron*-like alate extension (see Whatley and Zhao, 1987; plate 4, figs 21-22), which differs in shape from the more posterior and rounded ventral inflation of *L. (N.) pelius*. The genus *Heinzmalzia* Mostafawi, 1992 appears to have a close taxonomic affinity to the genus *Eocytheroperton* Alexander. Species of both these genera probably have discrete phylogenetic histories from species of the subgenus *Loxocythere (Novoloxocythere)*.

The type species of *Loxocythere (Novoloxocythere) – L. (N.) pelius* has a very similar subtriangular shaped inner margin to the Australian Cretaceous progonocytherid species' *Majungaella annula* Bate, 1972, *Majungaella verseyi* Neale, 1975, *Majungaella queenslandensis* Krömmelbein, 1975, *Majungaella ticka* (Krömmelbein, 1975) and *Majungaella scheibnerovae* (Krömmelbein, 1975) although these progonocytherids differ from *L. (N.) pelius* in internal view by having far more pronounced terminal hinge elements. A similar comparison can also be made between *L. (N.) pelius* and the African Cretaceous species *Majungaella nematis* Grekoff (*sensu* Dingle, 1984). However, in external view, Australian and African *Majungaella* species' differ significantly from *L. (N.) pelius* by possessing a circular reticulate ornament and strongly compressed anterior margins.

Loxocythere (Novoloxocythere) pilcus sp. nov.
Fig. 1 A-H; Fig 2.

1987 *Loxocythere* sp. 4 Warne, p. 441

Holotype: Adult, right valve, female, P122293.

Type Locality: Warneet Sands (*sensu* Warne, 1987) in the Geological Survey of Victoria borehole Sherwood 18 between the intervals 20m and 22m, 30°12', 145°16'E.

Etymology: Pileus (Latin) – cap or hat. A reference to this species being shaped like a cap.

Material. Twenty-five mostly disarticulated adult and juvenile valves from the mid Miocene Sherwood Formation, and latest Miocene and / or Early Pliocene Sandringham Sand (basal Black Rock Sandstone), Moorabool Viaduct Formation and Warneet Sands of south-central Victoria. All type specimens, including those illustrated here, are from the Warneet Sands (*sensu* Warne, 1987, 1993).

Diagnosis: A large, heavily reticulate species with large fossae and two to three submarginal ridges parallel to the anterior, ventral and posteroventral margins. Inner margin has a sub-triangular shape and posterodorsal margin is relatively short for genus.

Description: Carapace large (for genus), subtriangular and very thick shelled with coarsely reticulate ornament including large fossae and two to three submarginal ridges parallel to the anterior, ventral and posteroventral margins. There is some variability in the degree of ridge development between adult specimens. Ventrally, the carapace is strongly inflated. From an internal perspective the outer margin is subtriangular. Left valve larger than right valve and overlapping it. Unlike some *Loxocythere* species (i.e. *Loxocythere (L.) crassa*), the right valve does not protrude beyond the extremity of the left valve in the posterior. Left valve with broadly asymmetrically rounded anterior; convex anterodorsal and anteroventral slopes; extremity below mid-height. Posteriorly, left valve is acutely rounded (from an internal perspective) with short convex posterodorsal slope, curving down to meet the posteroventral and ventral margin in a smooth arc. Externally, the posterior margin is obscured by the posterior protruding ventral inflation. Left valve posterior extremity well above mid-height. Left valve dorsal margin straight to slightly convex. Right valve similar to left valve except dorsal margin is more strongly arched with a slightly longer posterodorsal margin and the extremity occurring just above mid-height. Maximum length slightly above mid-height; maximum height anterior of mid length; maximum width distinctly ventral and posterior of mid-length. Normal pore canals are sieve-type with some variability in size. Inner lamellae medium sized with small vestibula; marginal pore canals straight and scattered; broader at base. Hinge merodont with a smooth left valve hinge bar. Anterior and posterior right valve terminal teeth consist of three small lobes that lock into three sockets in the left valve. Adductors consisting of a vertical row of four elliptical scars. Frontal scar irregularly rounded. Sexual dimorphism evident in adults and late stage juveniles with males having a narrower posterior in lateral view than females.

Dimensions. Holotype, right valve, female, P122293, length = 0.53mm, height = 0.32mm, Paratype, left valve, male, P311645, length = 0.53mm, height = 0.31mm, Paratype, left valve, male, P122292, length = 0.52mm, height = 0.32mm, Paratype, left valve, juvenile female?, P122290, length = 0.51mm, height =0.31mm, Paratype, right valve, juvenile female?, P122291, length = 0.50mm, height = 0.31mm, Paratype, right valve, juvenile female?, P122295, length = 0.50mm, height = 0.29mm.

Remarks. This speeies has a distinetly different shape to *Loxocythere (L.) crassa* Hornibrook, 1952, the only other very heavily ornamented speeies of this genus. Aside from possessing eoarser ornament *L. (N.) pelius* differs from *L. (N.) kerryswansoni* in laeking a strongly eoneave mid ventral inner margin and a strongly upturned LV eaudal proeess. The posterior inner lamella in *L. (N.) pelius* is much narrower than found in speeies of *Eucytherura* Müller, 1894. *L. (N.) pelius* is superficially similar in shape to some loxoeonchid speeies sueh as *Loxoconcha variolata* Brady, although the former differs from the latter by possessing a greatly inflated posteroventral region and in laeking any semblanee of a gongylodont hinge (even though thiek shelled). The known age and lithostratigraphical range of *L. (N.) pelius* eurrently extends from mid Mioeene sandy faeies of the Sherwood Formation (Western Port Basin, Vietoria) to the latest Miocene and / or Early Plioeene sandy faeies of the Blaek Rock Sandstone, Moorabool Viaduet Formation (Port Phillip Basin) and Warneet Sands (Western Port Basin).

ACKNOWLEDGEMENTS

I aeknowledge diseussions on the genus *Loxocythere* with the late K. G. MeKenzie. Finaneial support and faeilities provided by Deakin University enabled the eompletion of the researeh presented in this paper. The Reeent New Zealand speeimens illustrated here were originally colleeted by N. de B. Hornibrook and were passed onto me by K.G. MeKenzie. The Auekland Museum is thanked for a loan of the type speeimens of *L. kingi*. Reviewers of this manuseript are thanked for their detailed and eonstruetive eomments.

REFERENCES

Athersuch, J. & Horne, D.J., 1984. A Review of some European genera of the Family Loxoeonehidae (Crustaeea: Ostraeoda). *Zoological Journal of The Linnean Society* 81: 1-22.

Baird, W., 1850. The natural history of the British Enstomostraca. *Royal Society of London (1850),* 1-364.

Bate, R.H., 1972. Upper Cretaeeous Ostraeoda from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology* 10: 1-85, pl.1-27.

Benson, R.H., 1964. Reeent eytheraeean ostraeodes from MeMurdo Sound and the Ross Sea, Antaretiea. *The University of Kansas Paleontological Contributions,* Arthropoda Artiele 6: 1-37.

Chapman, F., 1914. Deseription of new and rare fossils obtained by deep borings in the Mallee. Part 3. Ostraeoda to fishes. *Proeeedings of the Royal Society of Victoria* 27: 28-71, pl. 6-10.

Dingle, R.V., 1984. Mid-Cretaceous Ostraeoda from southern Africa and the Falkland Plateau. *Annals of the South African Museum* 93(3): 97-211.

Hanai, T., 1959. Studies on the Ostraeoda from Japan V. Subfamily Cytherinae Dana, 1852 (emend.). *Journal of the Faculty of Science, University of Tokyo sec 2,* 11(4): 409-418.

Hartmann, G., 1982. Beitrag zur Ostraeodenfauna Neuseelands (mit einem Naehtrag zur Ostraeodenfauna der Westküste Australiens). *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 79: 119-150.

Hartmann, G., 1986. Antarktisehe benthisehe Ostraeoden 1 (Mit einer Tabelle der bislang aus der Antarktis bekannten Ostraeoden). Auswertung der Fahrten der "Polarstern" Ant 111/2 (Sibex-Sehnitte) und der Reise 68/1 der "Walther Herwig" (1. Teil: Elephant Island) in die Antarktis. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 83: 147-221.

Hartmann, G., 1987. Antarktische benthisehe Ostraeoden 11. Auswertung der Fahrten der "Polarstern" Ant 111/2 (Sibex-Sehnitte) und der Reise der "Walther Herwig" 68/1 und 2. 2. Teil: Elephant Island und Bransfield-Staße. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 84: 115-156.

HARTMANN, G., 1989. Antarktische benthische Ostracoden V. Auswertung der Südwinterreise von FS "Polarstern" (Ps9/V-1) im Bereich Elephant Island und der Antarktischen Halbinsel. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 86: 231-288.

HORNIBROOK, N. DE B., 1952. Tertiary and Recent marine Ostracoda of New Zealand: Their Origin, Affinities and Distribution. *New Zealand Geological Survey, Palaeontological Bulletin* 18: 1-82.

JENKINS, J. J., 1962. The geology and hydrogeology of the Western Port area. *Geological Survey of Victoria: Underground Water Investigation Report* 5, 1-81.

KRÖMMELBEIN, K., 1975. Ostracoden aus der Kreide des Great Aretesian Basin, Queensland, Australien. *Senckenbergiana lethaea* 55 (6): 455-483.

LATREILLE, P.A., 1806. *Genera crustaceorum et inseactorum.* Koenig, Paris, 4 parts in 2 volumes, 217-583.

MCKENZIE, K.G., 1967. Recent Ostracoda from Port Phillip Bay, Victoria. *Proceedings of the Royal Society of Victoria* 80 (1): 61-106.

MCKENZIE, K.G., REYMENT, R.A. & REYMENT, E., 1993. Eocene Ostracoda from the Browns Creek Clays from Browns Creek and Castle Cove, Victoria, Australia. *Revista Española de Palaeontologia* 8(1): 75-116.

MOSTAFAWI, N., 1992. Rezente Ostracoden aus dem mittleren Sunda-Schelf, zwischen der Malaiischen Halbinsel und Borneo. *Senckenbergiana lethaea* 72: 129-168.

MÜLLER, G.W., 1894. Die Ostracoden des Golfes von Neapel und der angrenzenden Meeres Meeresabschnitte. *Naples Stazione Zoologia, Fauna und Flora des Golfes von Neapel,* Monograph 31: 1-104.

MÜLLER, G.W., 1908. Die Ostracoden der deutschen Südpolar-Expedition 1901-1903. Deutsche Südpolar-Expedition 1901-1903, in Auftrage des Reichsamtes des Innern, herausgegeben von E. von Drygaliski, Berlin, 10, *Zoologie* 2: 51-181.

NEALE, J.W., 1967. An ostracod fauna from Halley Bay, Coates Land, British Antaretic Territory. *British Antaretic Survey Scientific Reports* 58: 1-50.

NEALE, J.W., 1975. The ostracod fauna from the Santonian ehalk (Upper Cretaceous) of Gin Gin, Western Australia. *Special Papers in Palaeontology* 16: 1-81, pl. 1-22.

NEIL, J.V. 2000. A Recent ostracode assemblage from Erith Island, Bass Strait, southern Australia – geographical and ecological comparisons, with a description of a new species of *Rotundracythere* (Ostracoda: Crustacea). *Proceedings of the Royal Society of Victoria* 112(2): 119-132.

SARS, G.O., 1866. Oversigt of Norges marine ostracoder. *Forhandlinger i Videnskabsselskabet i Kristiania, 1865,* 1-130.

WARNE, M.T., 1987. Lithostratigraphical associations of the ostracode fauna in the marine Neogene of the Port Phillip and Western Port Basins, Victoria, southeastern Australia. In *Shallow Tethys 2,* K.G. McKenzie, ed., Balkema, Rotterdam, 435-445.

WARNE, M.T., 1993. Micropalaeontological evaluation of eustatic and tectonic influences on Late Tertiary marine sedimentation within the Port Phillip at Western Port Basins, Victoria, Australia. In: McKenzie, K.G., Jones, P.J. (Eds.). *Ostracoda in the Earth and Life Sciences; Proceedings of the Eleventh International Symposium on Ostracoda, Warrnambool, Victoria, Australia 1991.* A. A. Balkema, Rotterdam, Netherlands. 259 - 275.

WARNE, M.T., 2002. Palaeo-Geomorphological significance of Miocene and Pliocene euryhaline Ostracoda in the Nepean 1 borehole, Port Phillip Basin, SE Australia. *Memoirs of the Australasian Association of Palaeontologists* 27: 139-148.

WARNE, M.T., 2004. Observations on *Loxocythere (Loxocythere) onyenensis* (Chapman, 1914) (Ostracoda) from the Cenozoic of S.E. Australia with comments on species attributed to *Microcytherura* Müller, 1894 and *Hemiparvocythere* Hartmann, 1982 from Australian and New Zealand marine waters. *Proceedings of the Royal Society of Victoria. (in press).*

WHATLEY, R.C. & CUSMINSKY, G., 2002. Upper Pliocene Ostracoda from the Burdwood Bank, SW Atlantic. *Revista Española de Micropalaeontologia* 34(1): 53-80.

WHATLEY, R.C., MOGUILEVSKY, A., RAMOS, M.I.F. & COXILL, D.J., 1988. The ostracod family Cytheruridae from the Antaretic and south west Atlantic. *Revista Española de*

Micropalaeontología 20: 171-203.

WHATLEY, R.C., MOGUILEVSKY, A., RAMOS, M.I.F. & COXILL, D.J., 1998. Recent deep and shallow water Ostracoda from the Antarctic Peninsula and the Scotia Sea. *Revista Española de Micropalaeontología* 30(3): 111-135.

WHATLEY, R., MOGUILEVSKY, A., TOY, N., CHADWICK, J. & RAMOS, M.I.F., 1997. Ostracoda from the south west Atlantic. Part 2. The littoral fauna from between Tierra del Fuego and the Río de la Plata. *Revista Española de Micropalaeontología* 29(2): 5-83.

WHATLEY, R. & ZHAO, Q., 1987. Recent Ostracoda of the Malacca Straits. *Revista Española de Micropaleontología* 19 (3): 327-366.

YASSINI, I. & JONES, B.G., 1995. *Foraminiferida and Ostracoda from estuarine and shelf environments on the southeastern coast of Australia.* The University of Wollongong Press, Wollongong, Australia, 1-484.

Manuscript received 12 January 2004
Manuscript accepted 5 November 2004

OBSERVATIONS ON *LOXOCYTHERE (LOXOCYTHERE) OUYENENSIS* (CHAPMAN, 1914) (OSTRACODA) FROM THE CENOZOIC OF S.E. AUSTRALIA WITH COMMENTS ON SPECIES ATTRIBUTED TO *MICROCYTHERURA* MÜLLER, 1894 AND *HEMIPARVOCYTHERE* HARTMANN, 1982 FROM AUSTRALIAN AND NEW ZEALAND MARINE WATERS.

MARK THOMAS WARNE

School of Ecology and Environment, Deakin University (Melbourne Campus), 221 Burwood Highway, Burwood, Victoria 3125, Australia.

WARNE, M.T., 2004:12:04. Observations on *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) (Ostracoda) from the Cenozoic of S.E. Australia with comments on species attributed to *Microcytherura* Müller, 1894 and *Hemiparvocythere* Hartmann, 1982 from Australian and New Zealand marine waters. *Proceedings of the Royal Society of Victoria* 116(2): 243-250. ISSN 0035-9211.

The type material of *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) from mid Cenozoic strata of the Mallee Bore No. 11 in the Murray Basin, S.E. Australia is partially redescribed and refigured. This species belongs to a discrete group of large elongate Cenozoic fossil and living *Loxocythere* species, the carapaces of which possess sub-rectangular inner margin outlines, and broadly rounded posterior extremities. Some much smaller but otherwise very similarly shaped species, that have previously been placed under the genus *Microcytherura* (i.e. *Microcytherura? peterroyi* Yassini and Jones, 1995) or the genus *Hemiparvocythere* Hartmann, 1982 (i.e. *Hemiparvocythere lagunicola* Hartmann, 1982), are also known from marine Cenozoic strata and modern seas of the Australasian region. There is a marked difference in the shape of the inner margin between this group of small Australasian forms and European species of *Microcytherura s.s.*. The former have broadly rounded posterior inner margins, whilst the latter have acutely rounded posterior inner margins. The latter also usually present posterior extremities located well below mid carapace height. It is here argued that this difference in inner margin shape between smaller Australasian species such as *Microcytherura? peterroyi*, and European species of *Microcytherura s. s.*, suggests that there is not a direct phylogenetic relationship between these two species groups.

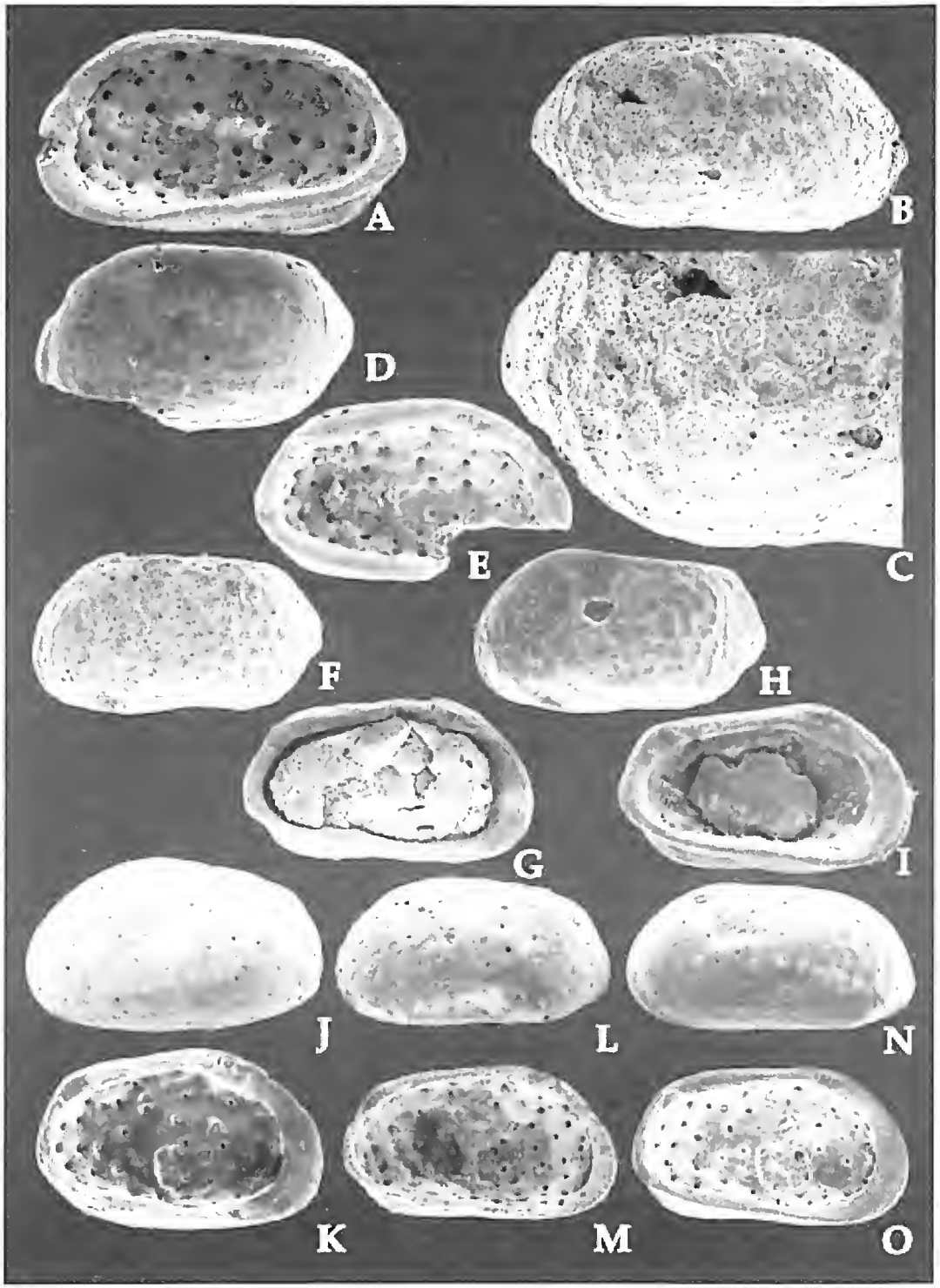
Key words: Ostracoda, *Loxocythere (Loxocythere) ouyenensis*, *Microcytherura*, *Hemiparvocythere*, Cenozoic, Australia, New Zealand

A VARIETY of species groups attributed to the genera *Loxocythere* Hornibrook, 1952 or *Microcytherura* Müller, 1894 have existed in Australasian marine waters throughout the Cenozoic and into the modern day. Previously, larger species have generally been assigned to the genus *Loxocythere* and smaller species to the genus *Microcytherura* (see also discussion in Warne, 2004). This paper will firstly describe the various species groups of the genus / subgenus *Loxocythere (Loxocythere)*. Secondly, the phylogenetic relationship between some elongate *Loxocythere (Loxocythere)* species and some similarly shaped but smaller Australasian species, variously attributed to the genera *Microcytherura* and *Hemiparvocythere* Hartmann, 1982, will be discussed. Thirdly, the type material of species *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) will be reviewed. Specimens illustrated herein are housed in Museum Victoria and have the registration numbers, P12529, P122297, P311646 - P311652.

COMPARATIVE MORPHOLOGY

Loxocythere (Loxocythere) Hornibrook, 1952

There are three types or groups of species here recognised under the genus / subgenus *Loxocythere (Loxocythere)*. The first, is the *Loxocythere* type species *L. (L.) crassa* Hornibrook, 1952, which has a thick shell, rugged reticulate ornament, subquadrate shaped inner margin and posterior extremity below mid height. The second group, which includes *L. (L.) kingi* Hornibrook, 1952 and *L. (L.) variasculpta* Whatley *et. al.*, 1997, have subdued ornament, relatively elon-


A
B
D
C
E
F
H
G
I
J
L
N
K
M
O

gate subrectangular carapaces / inner margins, and acutely rounded posterior outlines with valve posterior extremities well below mid height. The third group includes the species *L.(L.) hornibrooki* McKenzie, 1967 , *L.(L.) ouyenensis* (Chapman, 1914), *L. (L.) inflata* Hanai, 1959 and *L. (L.)* sp. (this study), which also have relatively elongate subrectangular carapaces and inner margin outlines, but differ from other groups of *Loxocythere (Loxocythere)* species by possessing broadly rounded posterior extremities. This group of species is transitional in carapace morphology between *Loxocythere (L.) crassa* and species of the genus *Cythere* O. F. Müller, 1785 (see Hanai, 1959, p. 414-415; plate 28). Thus, *Loxocythere (Loxocythere)* species in groups two and three can be distinguished from *L. (L.) crassa* by possessing relatively elongate carapaces. Further, *Loxocythere (Loxocythere)* species in groups two and three can be distinguished from each other by differences in the shape of the posterior inner margin. These species groups are not designated as separate subgenera because the carapace shape differences that are used here to delineate species groups are rather gradational in nature. Species of *Loxocythere (Novoloxocythere)* Warne, 2004 can be clearly distinguished from *Loxocythere (Loxocythere)* spp. as the former possesses posterior extremities well above mid height (i.e. adjacent to the dorsal margin).

The species *L. (L.) crassa* is only known from the New Zealand region. Species in *Loxocythere (Loxocythere)* group two have been variously recorded from shallow marine waters or sedimentary facies of the New Zealand and Antarctic regions, and from the south-west Atlantic continental shelf. Species in *Loxocythere (Loxocythere)* group three are known from the western Pacific region, current records being from coastal Australasia and Japan.

Microcytherura G. W. Müller, 1894

The genus *Microcytherura* was originally established to accommodate European ostracod specimens with *Microcytherura nigrescens* G. W. Müller, 1894 being designated as the type species. A distinctive carapace characteristic of this species and other European species of *Microcytherura* such as *M. fulva* (Brady and Robertson, 1874) and *M. angulosa* (Seguenza 1880), is a strong oblique dorsal truncation of the posterior margin (see fig 2 A-D). These delicately ornamented species possess posterior extremities near or below mid carapace height and possess an acutely rounded and elongated posterior margin with a relatively small angle between a short posteroventral margin and longer posterodorsal margin. Species with this type of posterior carapace shape and delicate carapace surface ornament occur in European and nearby seas, and can be considered as one distinctive species group within the genus *Microcytherura*. One Australian species, *Microcytherura sulcata* Yassini and Jones, 1995, is similar in general shape to European *Microcytherura* spp., although differs by possessing a strongly ornamented carapace. In general shape and ornament *M. sulcata* resembles various west African species such as *Microcytherura reticulata* Hartmann, 1974 and *Microcytherura ornata* Jellinek, 1993. These three Australian / west African species make up a second, very distinctive group of species, within the genus *Microcytherura*. On the basis of similarities in carapace shape (in particular the presence of acutely rounded posteriors) these two *Microcytherura* species groups as outlined above are here considered to have a close phylogenetic relationship.

Within Australian shallow marine environments there is a diversity of cytherid "species groups" that have been attributed to the genus *Microcytherura*. Aside from *M. sulcata*, few of the species in these groups have posterior carapace or inner margin shapes akin to those of European (or west African) *Microcytherura* species. One of these species groups, which includes the species *Microcytherura? peterroyi*

Fig. 1. A – C. *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914). Holotype, right valve, adult, male(?), P12529, from Mallee No.11 bore (267-270 feet), mid Cenozoic. A. Internal view, x 100. B. External view, x 100. C. External view of ornament in posteroventral region of carapace, x 200. D – E. *Loxocythere (Loxocythere)* sp. Left valve, adult, female(?), P311652, from Nepean 1 borehole (178.3 m), late Late Miocene. D. External view, x 100. E. Internal view, x 100. F – G. *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914). Left valve, juvenile, male, P311646, nodule bed at base of Sandringham Sand (Black Rock Sandstone) outcropping on sea bed 30 metres offshore from a point on the beach at the base of coastal cliffs between the Beaumaris Motor Yacht Squadron and the old Keefer's Boathouse, Beaumaris, Victoria, latest Miocene or earliest Pliocene. F. External view, x 100. G. Internal view, x 100. H – I. *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914). Left valve, juvenile, female, P122297, from Koo-wee-rup 14 (87– 113 m), early Middle Miocene. H. External view, x 100. I. Internal view, x 100. J – K. *Microcytherura?* sp. Left valve, adult, female, P311647, from Sherwood 18 (20m – 22 m), late Late Miocene. J. External view, x 100. K. Internal view, x 100. L – M. *Microcytherura?* sp. Left valve, adult, male, P311648, from Sherwood 18 (20m – 22 m), late Late Miocene. L. External view, x 100. M. Internal view, x 100. N – O. *Microcytherura?* sp. Left valve, adult, male, P311649, from Nepean 1 (178.3m), late Late Miocene. N. External view, x 100. O. Internal view, x 100.

Yassini and Jones, 1995, *Microcytherura? aestuaricola* Hartmann, 1980, *Microcytherura? triebeli* McKenzie, 1967 and *Mieroeytherura?* sp. (this study, Figs. 1J-O), possess broadly rounded posteriors with posterior extremities around (or slightly above / below) mid height. These posterior carapace shape characteristics are in contrast to those of European *Microcytherura* species, but are very similar to the posterior outlines of some (larger) species belonging to the genus *Loxocythere (Loxocythere)* such as *L. (L.) onyenensis* (see Plates 1 & 2). It is here argued that the difference in inner margin shape between this group of Australasian "*Microcytherura*" species (with broadly rounded posterior margins), and species of *Microcytherura s.s.*, (i.e. European forms), suggests that there is not a direct phylogenetic relationship between these two species groups. Australasian species, such as *Microcytherura? peterroyi*, are herein thought to have evolved from ancestral stock allied to elongate *Loxocythere (Loxocythere)* species such as *L. (L.) onyenensis* and as a result, considered examples of evolutionary modifications related to changes in carapace size. As a consequence, the genus *Micro-cytherura*, as it is generally and broadly applied to both European and Australian ostracod faunas, appears to be a polyphyletic taxon. However, if only applied to the European species (i.e. *M. nigreseens*, *M. fulva* and *M. angulosa*), as well as perhaps Australian and west African species such as *M. suleata*, this genus may represent a monophyletic cluster of species. The latter taxonomic framework is here considered preferable, although a full taxonomic review of Australian "*Microcytherura*" species is beyond the scope of this paper.

As illustrated here, particularly significant morphological similarities occur between juvenile valves of *Loxocythere (Loxocythere) onyenensis* (i.e. Figs. 1 F - I) and adult specimens of the Australian taxon *Microcytherura?* sp. (Figs. 1J - O), although the latter tend to have slightly lower and less conspicuously caudate posterior extremities (just below mid-height). This observation suggests that paedomorphic processes, initially operating in *Loxocythere* "ancestral stock", may have contributed to the radiation and diversification of some smaller Australian Cenozoic groups of so-called *Microcytherura* species.

Hemiparvocythere Hartmann, 1980

Some very small Australasian species belonging to the family Parvocytheridae Hartmann, 1959 (for example *Hemiparvocythere lagunicola* Hartmann, 1982), are also similar in carapace morphology to larger Australian Cenozoic *Loxocythere (Loxocythere)* species, although there are marked differences in the soft part anatomy. In the Parvocytheridae, there is a reduction from three walking appendages (maxilla and two thoracic legs) to only two (maxilla and one thoracic leg) reflecting adaptation to an interstitial environment (Hartmann and Puri, 1974). Despite this substantial difference in soft part anatomy, Hartmann and Puri (1974) commented that there is a close phylogenetic relationship between the Cytheridae

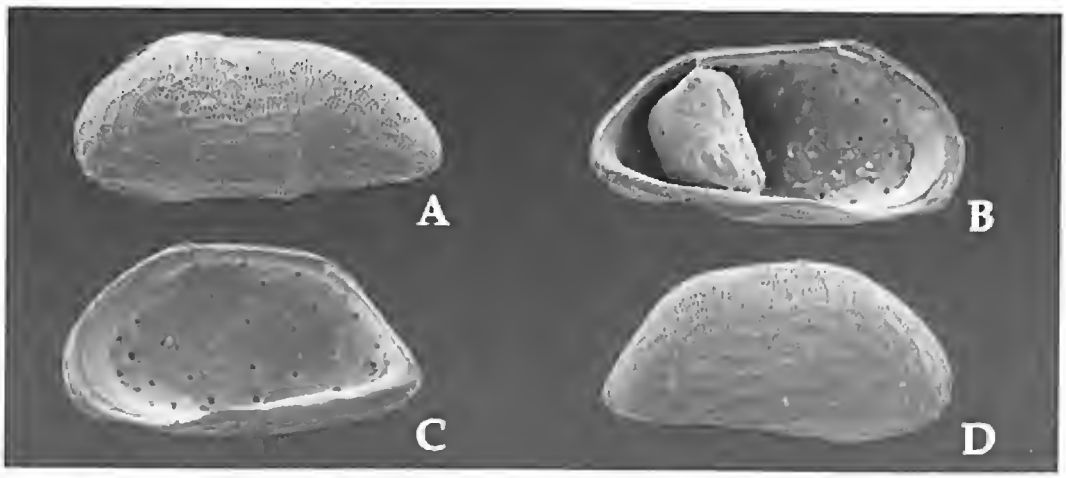


Fig. 2. *Microcytherura angulosa* (Seguenza, 1880) Specimens are from the seabed of the Adriatic Sea, Recent. A. Left valve, male, external view, P311650, x 100. B. Left valve, male, internal view, P311650, x100. C. Right valve, female, internal view, P311651, x 100. D. Right valve, female, external view, P311651, x 100.

Baird, 1850 and Parvocytheridae, the latter probably being derived from the former. The implication from this analysis by Hartmann and Puri (1974) is that close phylogenetic relationships are not always completely reflected in soft part anatomy, but rather may be more obvious in morphologically conservative carapace characters.

SYSTEMATIC PALAEONTOLOGY

Subclass Ostracoda Latreille, 1806
Order Podocopida G.W. Müller, 1894
Suborder Podocopina Sars, 1866
Superfamily Cytheracea Baird, 1850
Family Cytheridae Baird, 1850
Subfamily Cytherinae Baird, 1850

Remarks: Most authors place the genus *Mierocytherura s.s.* (European species') within the Cytheridae Baird (i.e. Jellinek, 1993), although as discussed by van Morkhoven, 1963, there is good evidence for the genus being placed within the Cytheruridae Müller, 1894. The latter view brings into question the often assumed close taxonomic relationship between *Loxocythere* and *Microcytherura* (i.e. Howe and McKenzie, 1989; Hartmann, 1982; McKenzie *et. al.*, 1993; Yassini and Jones, 1995). This controversy is not here resolved. However it is the view of the present author that European species of *Mierocytherura* are congeneric with the more robustly ornamented west African species *M. reticulata* and *M. ornata,* and one Australian species, *M. sulcata.* Members of this ornate group of *Mierocytherura* species, and the European species *Mieroeytherura angulosa,* (Seguenza, 1880) bear a close resemblance in inner margin outline to the New Zealand species *Loxocythere (Loxocythere) kingi.* All these species have a relatively elongated carapace posterior that is acutely rounded, the extermity of which is positioned adjacent to, or near, the ventral margin. This observation suggests that a common family level taxonomic association is warranted for the genera *Microcytherura* and *Loxocythere.*

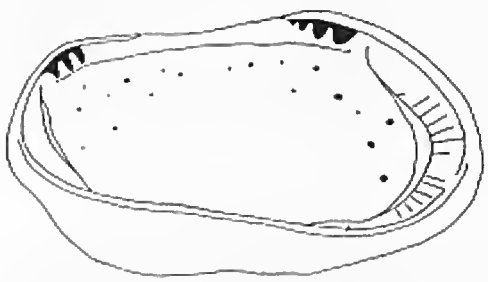


Fig. 3 *Loxocythere (Loxocythere) ouyenensis* Chapman, 1914; line drawing, left valve, juvenile, female(?), internal view, P122297, from Koo-wee-rup 14 (87– 113 m), early Middle Miocene, x 150.

Whilst most Cytherinae species possess a relatively simple merodont (hemimerodont or antimerodont) hinge, some species such as *Loxocythere (L.) crassa* Hornibrook, 1952 have pentodont – like terminal thickenings of the medium hinge element (pseudopentodont hinge sensu Warne, 1996; see Hartmann 1982, Pl. 1, figs. 7 & 8). A pseudopentodont hinge is also apparent in the species *Microcytherura angulosa* (figs. 2B and 2C herein; see also Bonaduce et. al., 1975, Pl. 46, figs 4 -6). However, for these two species, this medium hinge feature is associated with typically crenulated or lobed, and overall subrectangular shaped cytherine posterior hinge elements, and not with the generally smooth, rounded or arched posterior hinge elements characteristic of the true pentodont hinges; the latter as usually found in leptocytherid species belonging to the subfamily Pectocytherinae Hanai, 1957. Similarly, the parvocytherid *Hemiparvocythere lagunicola* Hartmann, 1982 also displays terminal thickening of the medium hinge element (Hartmann, 1982; Plate 5, figures, 4 & 5).

Genus **Loxocythere** Hornibrook, 1952
Subgenus **Loxocythere** Hornibrook, 1952
Type species, *Loxocythere crassa* Hornibrook, 1952

Remarks: Prior to the present study, a number of taxonomic schemes had been proposed for the genera *Microcytherura* Müller, 1894, *Tetracytherura* Ruggieri, 1952 and *Loxocythere* Hornibrook, 1952. Ruggieri (1959) and Hanai (1957) regarded *Tetracytherura* [type species = *M. angulosa* (Seguenza, 1880)] as a junior synonym of *Loxocythere* while van Morkhoven (1963) and Hartmann (1979) regarded *Tetracytherura* as a junior synonym of *Mierocytherura.* McKenzie (1967) and Bonaduce *et. al.* (1975) maintained it as a separate genus. Whilst the type species of the genus *Tetracytherura* is much less elongate than the type species of *Microcytherura,* it is here considered that this morphology difference is insufficient in extent to recognise two separate gen-

era. Hartmann (1980) considered *Loxocythere* a subgenus of *Microcytherura*, with *Microcytherura (Microcytherura)* being smaller and possessing only one type of normal pore canal, and *Microcytherura (Loxocythere)* being relatively large and possessing three types of normal pore canal. However, given the problematic family level taxonomic relationship between *Microcytherura* and *Loxocythere* (see above discussion) it would seem appropriate for the present to regard both as discrete genera. Some European loxoconchid species, such as *Elofsonia baltica* (Hirschmann), are convergent in carapace morphology towards some elongate *Loxocythere* species, although the former are generally thin shelled and less ventrally inflated.

Loxocythere (Loxocythere) ouyenensis
(Chapman, 1914)
Figs. 1A-C, F-I; 3.

1914 *Cytherura ouyenensis* Chapman, p. 44 -45, pl.8, figs. 35a,b
1916 *Cytherura ouyenensis* Chapman, p. 379, pl. 74, figs. 35a & b
1981 *Loxocythere ouyenensis* Chapman, McKenzie, p. 106.
1987 *Loxocythere* sp.6 Warne, p.441.

Holotype: Adult, right valve, P12529

Type Locality: Mallee Bore 11 at 267 -270 feet (see Chapman 1914 for further details)

Material. The type specimen is from subsurface mid Cenozoic marls of the Murray Basin, Victoria, Australia (Fig. 1 A-C). Additional, mostly juvenile specimens examined for this study come from mid Miocene and Late Miocene shallow marine sand facies of the Port Phillip and Western Port Basins (Figs. 1F-I;3). Details of localities in the Port Phillip Basin and the Western Port Basin that are listed in the figure captions can be found in Warne, 1993 and 2002.

Additional description: The following comments are modifications or expansions of descriptive comments provided by Chapman, 1914 (p. 44 - 45). Carapace large, elongate, subrectangular and thick shelled with a faint, reticulate ornament (varies in strength between specimens). Carapace with posteroventral inflation that slightly overhangs the posteroventral margin. Posterior extremity of RV at about mid-height and slightly caudate; anterior extremity slightly below mid height. In RV maximum height anterior of mid length. Adductor muscle scar pattern consisting of a vertical row of four individual oblong scars. Inner margin well calcified in both adult and juvenile specimens. Normal pore canals numerous and very large, particularly as viewed from an internal perspective. Hinge is merodont with a smooth median element and laterally elongate and strongly crenulated terminal hinge elements.

Dimensions: Holotype, right valve, adult, P12529, length = 0.55 mm, height = 0.29 mm

Remarks: The dimensions of the holotype of *Loxocythere (Loxocythere) ouyenensis* recorded here are less than those recorded by Chapman, 1914. The Pleistocene S. E. Australian species *Loxocythere (L.) posteroventrobullata* McKenzie, *et. al.*, 1990 differs from *L.(L.) ouyenensis* only by possessing a slightly more inflated posteroventral margin; the former being a closely related descendant, or junior synonym of the latter. The latest Miocene S.E. Australian species *Loxocythere (Loxocythere)* sp. (Fig. 1 D – E) differs by possessing a smooth carapace (except for very faint reticulation in posterior third of carapace) and a greater height to length ratio.

ACKNOWLEDGEMENTS

Staff members at Museum Victoria are thanked for allowing access to the type specimen of *L. (L.) ouyenensis* illustrated in this paper. The late Dr K. G. McKenzie kindly passed onto the present author the illustrated specimens of *Microcytherura angulosa*, which were originally collected by G. Bonaduce from the Adriatic Sea. Financial assistance and facilities provided by Deakin University were used to support the research presented in this paper. Two reviewers of this paper are thanked for their input of opinions and constructive comments.

REFERENCES

Baird, W., 1850. The natural history of the British Entomostraca. *Royal Society of London (1850)*, 1-364.

Bonaduce, G., Ciampo, G. & Masoli, M., 1975. Distribution of Ostracoda in the Adriatic Sea.

Pubblicazioni della Stazione Zoologica di Napoli, volume 40, Suppl. 1, 1- 154.

Brady, G. S. & Robertson, D., 1874. Contributions to the study of the Entomostraca VI. On Ostracoda taken amongst the Scilly Islands, and on the anatomy of *Darwinella stevensoni*. *Annals and Magazine of Natural History* , Series 4(13): 114-119.

Chapman, F., 1914. Description of new and rare fossils obtained by deep boring in the Mallee. Part 3. Ostracoda to fishes. *Proceedings of the Royal Society of Victoria* 27: 28-71, pl. 6-10.

Chapman, F., 1916. Cainozoic geology of the Mallee and other Victorian bores. *Records of the Geological Survey of Victoria* 3 (4): 327-430, pl. 63-78.

Hanai, T., 1957. Studies on the Ostracoda from Japan II. Subfamily Pectocytherinae n. subfam.. *Journal of the Faculty of Science, University of Tokyo sec 2*, 10(3): 469-482.

Hanai, T., 1959. Studies on the Ostracoda from Japan V. Subfamily Cytherinae Dana, 1852 (emend.). *Journal of the Faculty of Science, University of Tokyo sec 2*, 11(4): 409-418.

Hartmann, G., 1959. Zur Kenntris der lotischen Lebensbereiche der pazifischen Küste von El Salvador unter besonder Berücksichtigung seiner Ostracoden-fauna. *Keiler Meeresforschungen* 15(2): 187-241; pl. 27-48.

Hartmann, G., 1974. Die Ostracoden des Untersuchungsgebiets. In: G. Hartmann – Schröder and G. Hartmann: Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Moçambique unter besonder Berücksichtigung der Polychaeten und Ostracoden. Teil 3., *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* Erg-Bd 69: 229-250.

Hartmann, G., 1979. Die Ostracoden der Ordnung Podocopida G.W. Müller, 1894 der warmtemperierten (antiborealen) West- und Südwestküste Australiens (zwischen Perth im Norden und Eucla im Süden). In *Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden, Tl. 3*, G. Hartmann & G. Hartmann-Schröder, eds. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 76: 219-301.

Hartmann, G., 1980. Die Ostracoden der Ordnung Podocopida G.W. Müller, 1894 der warmtemperierten und subtropisch-tropischen Küstenabschnitte der Süd- und Südostküste Australiens (zwischen Ceduna im Westen und Lakes Entrance im Osten) *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 77: 111-204.

Hartmann, G., 1982. Beitrag zur Ostracodenfauna Neuseelands (mit einem Nachtrag zur Ostracodenfauna der Westküste Australiens). *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 79: 119-150.

Hartmann, G. & Puri, H. S., 1974. Summary of neontological and palaeontological classification of Ostracoda. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 70: 7-73.

Hornibrook, N. DeB., 1952. Tertiary and Recent marine Ostracoda of New Zealand: Their Origin, Affinities and Distribution. *New Zealand Geological Survey, Palaeontological Bulletin* 18: 1-82.

Howe, H.V. & McKenzie, K.G., 1989. Recent marine Ostracoda (Crustacea) from Darwin and North-Western Australia. *Northern Territory Museum of Arts and Sciences*. Monograph 3: 1-50.

Jellinek, T., 1993. Zur Ökologie und Systematik rezenter Ostracoden aus dem Bereich des kenianischen Barriere-Riffs. *Senckenbergiana lethaea* 73(1), 83-225.

Latreille, P.A., 1806. Genera crustaceorum et inseactorum. Koenig, Paris, 4 parts in 2 volumes, 217-583.

McKenzie, K.G., 1967. Recent Ostracoda from Port Phillip Bay, Victoria. *Proceedings of the Royal Society of Victoria* 80 (1): 61-106.

McKenzie, K.G., 1981. Chapman's "Mallee Bores" and "Sorrento Bore" Ostracoda in the National Museum of Victoria, with the description of *Maddocksella* new genus. *Proceedings of the Royal Society of Victoria* 93: 105-107.

McKenzie, K.G., 1990. Pleistocene and Recent Ostracoda from Goose Lagoon Drain, Victoria and Kingston, South Australia. *Bulletin of the Geological Institutions of the University of Uppsala. N. S.*, volume 16: 1-46.

McKenzie, K.G., Reyment, R.A. & Reyment, E.R., 1993. Eocene Ostracoda from the Browns

Creek Clays at Browns Creek and Castle Cove, Victoria, Australia. *Revista Española de Palaeontología* 8(1): 75-116.

Müller, G. W., 1894. Die Ostracoden des Golfes von Neapel und der angrenzenden Meeres Meeresabschnitte. *Naples Stazione Zoologia, Fauna und Flora des Golfes von Neapel,* Monograph 31, 1-104.

Müller, O. F., 1785. *Entomostraca seu insecta testracea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconnbus illustravit.* Frankfurt, Lipsiae et Havniae, 1-135.

Ruggieri, G., 1952. Gli Ostracodi delle sabbie grigie quaternaire (Milazziano) di Imola II. *Giornale di Geologia* 22: 1-57.

Ruggieri, G., 1959. Enumerazione degli Ostracodi marini del Neogene, Quaternario e Recenti italiana descritti o elencati nell' ultimo decennio. *Atti Società Italiana di Scienze Naturali* 98: 183-208.

Sars, G.O., 1866. Oversigt of Norges marine ostracoder. *Forhandlinger i Videnskabsselskabet i Kristiania, 1865,* 1-130.

Seguenza, G., 1880. Le formazioni terziarie nella provincial di Reggio (Calanbria), Ostreodi. *Memorie della Reale Accademia dei Lincei, Classe di Scienze Fisiche, Matematiche e Naturali,* Serie 3, vol.6, 1-446.

Van Morkhoven, F.P.C.M., 1963. Post-Palaeozoic Ostracoda: Their Morphology, Taxonomy and Economic Use. Volume 2 (Generic Descriptions). *Elsevier,* Amsterdam, 1-478.

Warne, M.T., 1987. Lithostratigraphical associations of the ostracode fauna in the marine Neogene of the Port Phillip and Western Port Basins, Victoria, southeastern Australia. In *Shallow Tethys 2,* K.G. McKenzie, ed., Balkema, Rotterdam, 435-445.

Warne, M.T., 1993. Micropalaeontological evaluation of eustatic and tectonic influences on Late Tertiary marine sedimentation within the Port Phillip at Western Port Basins, Victoria, Australia. In *Ostracoda in the Earth and Life Sciences; Proceedings of the Eleventh International Symposium on Ostracoda, Warrnambool, Victoria, Australia 1991.* K.G. McKenzie & P.J. Jones, eds, A. A. Balkema, Rotterdam, Netherlands, 259 - 275.

Warne, M.T., 1996. The evolutionary development of hinge structures within the Mesozoic and Cainozoic ostracod families Cytheridae Baird, 1850 and Leptocytheridae Hanai, 1957. *Proceedings of the 2nd European Ostracodologists Meeting, Glasgow 1993.* British Micropalaeontological Society, London, 209 – 212.

Warne, M. T., 2002. Palaeo-Geomorphological significance of Miocene and Pliocene euryhaline Ostracoda in the Nepean 1 borehole, Port Phillip Basin, SE Australia. *Memoirs of the Australasian Association of Palaeontologists* 27: 139-148.

Warne, M. T. 2004. Description of *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov. (Ostracoda) from the Cenozoic of S.E. Australia with comments on species of *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 from Australian and Antarctic marine waters. *Proceedings of the Royal Society of Victoria* (*in press*).

Whatley, R., Moguilevsky, A., Toy, N., Chadwick, J. & Ramos, M. I. F., 1997. Ostracoda from the south west Atlantic. Part 2. The littoral fauna from between Tierra del Fuego and the Río de la Plata. *Revista Española de Micropalaeontología* 29(2): 5-83.

Yassini, I. & Jones, B.G., 1995. *Foraminiferida and Ostracoda from estuarine and shelf environments on the southeastern coast of Australia.* The University of Wollongong Press, Wollongong, Australia, 1-484.

Manuscript received 12 January 2004
Manuscript accepted 5 November 2004

EXECHONELLA (EXECHONELLIDAE: BRYOZOA, CHEILOSTOMATA) FROM THE RECENT AND MIOCENE OF SOUTHERN AUSTRALIA

P. L. Cook[1] & P. E. Bock[2]

[1] Honorary Associate, Marine Biology Section, Museum of Victoria, GPO Box 666E, Melbourne, VIC 3001, Australia.

[2] School of Ecology and Environment, Deakin University, Melbourne Campus, Burwood Highway, Burwood, Victoria 3125. email pbock@deakin.edu.au

Cook, Patricia L. & Bock, Philip E. 2004:12:04. *Exechonella* (Exechonellidae: Bryozoa, Cheilostomata) from the Recent and Miocene of southern Australia. *Proceedings of the Royal Society of Victoria* 116(2): 251-268. ISSN 0035-9211.

The cheilostome family Exechonellidae Harmer, 1957 is widely distributed in time and space. The genus *Exechonella* Duvergier, 1924 has a pan-tropical to subtropical distribution from the Eocene to the Recent and is represented by several Australian species from the Tertiary of Victoria and the Recent of the southern and eastern coasts. Some species exhibit a wide range of variation in morphological characters, and one, *Exechonella papillata,* appears to be new, and is described here. Nearly all specimens are encrusting, but one Tertiary Victorian species has erect, cylindrical, branching colonies. Recent samples, from a depth range of 40-190 metres, include large colonies of several thousand zooids. Frontal wall structures include marginal septular pores connecting between the visceral and hypostegal coeloms, and frontal foramina. Avicularia and homologous structures derived from frontal septular pores are illustrated. The structure of the frontal foramina in different populations of Tertiary *E. marginata,* demonstrates a major development of hypostegal coelom not found in other species, but resembling that found in another exechonellid genus, *Stephanopora* Kirkpatrick, 1888.

Keywords: Bryozoa, Cheilostomata, Exechonellidae, *Exechonella*, Australia, new taxa

HARMER (1957: 651) introduced the family Exechonellidae for *Exechonella* alone. He noted the umbonuloid nature of the frontal shield and listed a large number of Indo-west-Pacific localities for material he assigned, principally, to *E. tuberculata* (MacGillivray, 1883) and *E. magna* (MacGillivray, 1895) (see below). Duvergier (1924: 18) had introduced *Exechonella* with the type species, *Cyclicopora? grandis* Duvergier (1921: 124, pl. 3, figs 2,3), originally recorded from the Lower Miocene (Aquitanian) of the Gironde, France. Cheetham (1966: 62) noted that this was the type species by monotypy. He emphasised that the type species of *Exechonella* was not *Hiantopora magna* MacGillivray as stated by Canu & Bassler (1927: 4) and by Harmer (1957: 652). Cheetham commented "However irregular, Duvergier's introduction has priority". In addition, the selection by Vigneaux (1949) of "*C. grandis* Duvergier" as type species of his genus *Hippexechonella* means that the name is a junior objective synonym of *Exechonella.*

Several other genera have been assigned to the Exechonellidae, but all require a more complete examination of the morphology of their type, and any other relevant species, before their relationships can be established. They include *Anexechona* Osburn, for *A. ancorata* Osburn (1950: 96, pl. 11, fig. 1), from the Gulf of California. *A. ancorata* has large, vicarious avicularia, and the frontal shield has large pores. Colonies are encrusting and occasionally erect and adeoniform; ovicells and spines are lacking. Osburn described the ontogeny of the frontal shield as being similar to that of *Exechonella. Anarthropora* Smitt, 1868 (type species *Lepralia monodon* Busk, 1860) and *Triporula* Canu & Bassler, 1927 (type species *Escharipora stellata* Smitt, 1873) also have frontal shields with foramina and surrounding calcification similar to that in *Exechonella*; the structure of the orifice and peristome is similar in these three genera. *Xynexecha* Gordon & d'Hondt, for *X. pulchra* Gordon & d'Hondt (1997: 15, figs 8,9), from New Caledonia superficially resembles *Exechonella marginata* (see

below), and has erect, cylindrical eolonies, zooids with long, tubular peristomes, and a frontal shield with a restricted eentral area of foramina. However, this area is deseribed as umbonuloid, but surrounded by a "cryptocyst" with "arcolae". If this means a eryptoeystal (lepralioid) frontal shield, with marginal frontal septular pores, it is quite unlike that of *Exechonella*. Alternatively, it is difficult to understand how a eryptocyst (which is an interior wall growing into a pre-existent coelom), can have marginal frontal septular pores, and give rise to an umbonuloid shield. The caleification of the long, tubular peristome is deseribed as similar to that of the "eryptoeyst", but whether it is inferred to be umbonuloid or lepralioid, and the nature of its eoelomic relationships, are uncertain. Although obviously not elosely related, the shield resembles that of an araehnopusiid genus, *Briarachnia*, deseribed by Gordon (1984). It seems probable that, in spite of its appearanee, *X. pulchra* may not be referable to the Exeehonellidae. The genus *Stephanopora* Kirkpatriek (1888) was referred to the Exechon-ellidae by Hayward (1988), who redeseribed the type species, *S. cribrispinata* (Kirkpatriek, 1888) from Mauritius. Gordon (1993) expanded analysis of its morphology and added notes on *S. perelegans* (Harmer, 1957) from Indonesia. The eomplexity of the frontal spinose extensions of the umbonuloid shield obscures the similarities of these speeies to those of *Exechonella*, and is diseussed below (p. 00). Hayward (1988) also provisionally referred *Anarthropora horrida* Kirkpatriek (1888) to *Exechonella*. *A. horrida* has zooids with an umbonuloid frontal shield, long tubular peristomes, and sporadie, peduneulate avieularia. Although it appears to be generieally distinet from *Exechonella*, it eertainly shares many characteristies with other Exeehonellidae.

In eontrast, the genus *Coleopora* sensu strieto has little in eommon with *Exechonella*. *Coleopora* was introdueed by Canu & Bassler (1927, pl. 1, fig. 7) for a single "Reeent" species, *C. verrucosa*. Later, Canu & Bassler (1929: 267, pl. 20, fig. 4, pl. 26, fig. 9) redeseribed the same specimen (from Jolo in the Philippines, "Albatross" Station 5137). *Coleopora* was defined with a hyperstomial ovieell "never elosed by the operculum", and figured with a zooidal frontal "punctured by small very numerous tremopores". Among these were thiekened tubes, whieh were retouehed in the illustrations, but appear to be hollow, and vary in number from 3-9 per zooid. Although no ovieell was figured, it was stated that the speeies was "in reproduetion", and that the ovieell was "globular". Large foramina with a border, or raised edges, as in *Exechonella antillea* (Osburn, 1927) and *E. tuberculata* respeetively, did not oeeur. *Coleopora* was assigned to the family Petraliidae. Harmer (1957: 897, pl. 54, figs 11, 12), however, considered it to be a synonym of the Pleistoeene Italian genus *Teuchopora*, and assigned speeimens of his "*T.*" *verrucosa* from New Guinea to the Teuchoporidae. He deseribed the zooids with numerous small frontal pores and hollow papillae. Poluzzi (1977) redefined *Teuchopora* from type speeimens and demonstrated in detail its distinetion from *Coleopora*, as noted by Winston & Heimberg (1986: 15). Harmer (1957: 897) was uneertain of the affinities of his specimens and noted similarities with *Exechonella*. Winston & Heimberg (1986: 15, figs 33-34) deseribed *Coleopora verrucosa* from Bali, and referred the genus to Exeehonellidae. Their figures show zooid frontal shields with numerous, slit-like pores, interspersed with 3-4 seattered "hollow papillae". There is a marked contrast between their figures of *C. verrucosa* and those of *Exechonella brasiliensis* Canu & Bassler, 1928 (Winston & Heimberg, 1986: 15, figs 26, 27), whieh show large foramina with curved rims. Winston & Heimberg (1986: 16) noted that the species ineluded in *Coleopora* may not be a monophyletic group. Very few of these, ineluding the type species, seem to be referable to the Exeehonellidae. For example, *C. gigantea* Canu & Bassler (1923), redescribed by Osburn (1952), from the Pleistoeene and Reeent of California respectively, and *C. seriata* Canu & Bassler, 1929, from the Philippines, also deseribed by Hayward (1988) from Mauritius, have large, prominent imperforate ovieells and numerous small frontal pores. However, *C. erinacea* Canu & Bassler (1929: 268, pl.19, figs 5-8), has figures which are heavily retouched, and may refer to more than one speeies, but appears to be referable to *Exechonella* (see p.00). Very similar species of *Exechonella* oeeurred in North Ameriea in the Middle Eoeene, and were deseribed and figured by Canu & Bassler (1920), who originally referred them to other genera, but reassigned them later (Canu & Bassler 1929).

The stratigraphieally earliest species of the family appears to be *Cheilopora? orbifera* Canu & Bassler (1920: 526, pl. 14, fig. 16) from the Claibornian (Middle Eocene) of the USA, together with *Cyclicopora laticella* Canu & Bassler (1920: 427, pl. 55, fig. 6) and *Cheilopora prelucidioides* Canu & Bassler (1920: 527, pl. 68, figs 1,2) both from the Jacksonian (Late Eoeene). Cheetham (1966) recorded an almost contemporaneous, unnamed Eoeene form from the

Bartonian of the Upper Bracklesham beds of southern England. Names of other Tertiary species from France and Italy were given by Canu & Bassler (1929) and Cook (1985). More than 15 nominal species of *Exechonella* have been described, and there are more than 50 records of variously named and unnamed taxa.

Records of several nominal Recent species are virtually pantropical to subtropical in distribution, which suggests that they may each include more than one taxon. One problem is that relatively few distinctive characters are available for comparison among specimens. There is a wide range in variation of character states among the records from different localities, but an almost equally wide range occurs within populations from neighbouring localities. Harmer (1957), Cook (1985) and Fransen (1986) have all commented on this variability, and the consequent difficulty which exists in distinguishing taxa. Australian records of specimens referable to *Exechonella* fall very approximately, into four groups of species, each with similar morphologies. The first group is large and includes the type species, *E. grandis,* and other Tertiary European taxa, the world-wide *E. antillea*-complex, *E. brasiliensis* and the three Eocene forms from North America mentioned above. It is represented in Australia by a Recent species, *E. papillata* sp. nov. from the Great Australian Bight. The second group includes the *E. magna*-complex, which has an almost entirely Australian Tertiary and Recent distribution, but does include some records from the Philippines. The third group includes Australian and other records of Recent *E. tuberculata, E. discoidea* and *E. ampullacea.* The fourth group consists entirely of the Australian Tertiary *E. marginata*-complex. The Australian fauna therefore includes records of two Tertiary, and four Recent species or species-complexes.

MORPHOLOGY

There are relatively few diagnostic characters available for discrimination of species in *Exechonella.* In spite of this, *Exechonella* is an "easily recognised" genus. The colonies are usually encrusting, and unilaminar. Overgrowths may occur, as in the multilaminar *Exechonella papillata,* some bilaminar specimens of *E. magna* (which also includes a single lunulitiform colony), and the erect, quadriserial branches of the *E. marginata*-complex. The very large zooids may be distinguished with the naked eye, those of *E. papillata, E. marginata* and *E. antillea* usually exceeding 1.0 mm in length, and reaching 1.6 mm in *E. gigantea* Cook (1967: 339, pl. 2C, D) from west Africa. The ancestrulae are usually very small, but resemble later-budded zooids (Fransen 1986). Zooids are often budded singly, with little tendency to form part of a "growing edge" (see Cook 1985: 45), although a form of marginal growing zone does occur in *E. papillata* and *E. magna.*

The lateral septular pores of nearly all species are numerous and uniporous in all zooids which are deep vertically, like those of *E.* cf. *discoidea* and *E. papillata,* but are reduced to three series or less, in shallower zooids, such as those of *E. tuberculata* and *E. marginata.* The marginal septular pores provide communication between the visceral and hypostegal coeloms, and in most species remain visible throughout ontogeny, as in *E. magna,* where they may be prominent. They occur peripherally, and often distally to the peristome in a single series, but may also form groups at the proximal end, or in the lateral "corners" of zooids, as in *E. papillata* and *E. marginata.* In some species, with partially isolated, flask-like zooids, like *E.* cf. *discoidea,* they are extremely small, and occur close to the base of the exposed lateral faces of the zooids.

The frontal shield has umbonuloid ontogeny, which has been discussed in detail by Cheetham & Cook (1983) and Gordon (1993). Essentially, it consists of a fold of cuticle derived from the frontal marginal septular pores, growing above a pre-existing frontal membrane with contiguous operculum and fully developed and functional parietal muscles (Cook 1985). The basal-facing calcified surface of the fold is an exterior wall, and has an outer closely apposed cuticular surface. The upper-facing calcified surface of the frontal is an interior wall, with an overlying hypostegal coelom derived from marginal septular pores, beneath an investing cuticle.

The primary orifice is uncalcified and the early ontogeny of the calcified orifice resembles that of many "cribrimorphs" (Cook 1967), with an orificial bar, or even a peristome calcifying above the operculum before the rest of the shield is complete (Cook 1967, Gordon 1984). The resulting early calcified orifice is often a simple, almost circular structure; but in several species, an inner lamina on the distal side terminates laterally at the base of the peristome. This may be the "lining" mentioned by Harmer (1957: 655). The lateral ends of the lamina may appear as distinct, paired "condyles" (see Fransen 1986, fig. 29a, b) (Fig. 1B), or as "pockets" within the calcification (Fig. 3D). In species with long, tubular peristomes these are not usually observable. Orifices may vary markedly

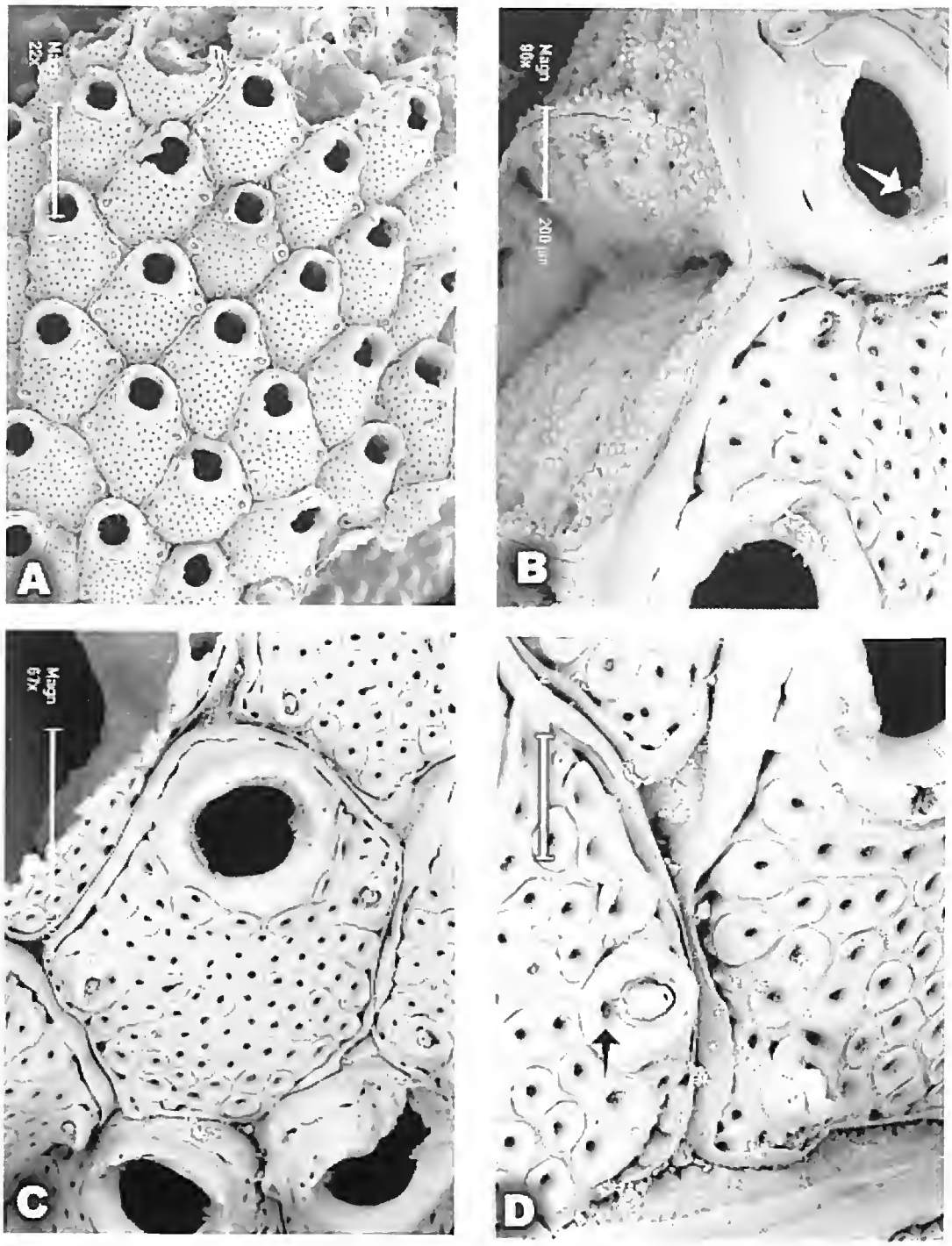


Fig. 1. A-D, *Exechonella papillata* sp. nov. NMV F97951, holotype, GAB Station 110. A. Zooids showing frontal shield with numerous foramina, calcified orifice with thickened peristome. Note raised zooid margins and lateral kenozooids, x17. B. Lateral vertical walls showing numerous uniporous septular pores, and frontal shield with thickened foraminal margins. Note small foramen associated with lateral kenozooid. Arrow points to edge of lamina in orifice, x67. C. Detail of zooid with distal lamina in orifice, two kenozooids. Note relation between marginal communication pores and zooid margin, x48. D. Detail of papillate kenozooid on left-hand zooid. Arrow points to adjacent foramen, x72.

within nominal taxa. For example, the orifices of *E. antillea* figured by Hayward (1974, Fig. 4C) from Chios, and by Winston (1982, fig. 60) from Florida, are far narrower proximally to the "condyles" than the orifices of *E. antillea* illustrated by Fransen (1986, fig. 29a, b), from the type region of Curaçao, and from Ghana by Cook (1985, pl. 15, A, B). In addition, "condyles" are absent in most colonies of Recent *E. magna*, but present in one Miocene population, at least, of the same nominal species. Peristomes may be raised, with irregular spinous projections on their margin, or be tubular and prominent, sometimes flaring outward terminally. Calcification is smooth on the inner surface, which is directly derived from the lower face of the calcified shield, and is part of the exterior wall. It is granular on the outer surface, which is an extension of the upper surface of the shield and is an interior wall, capable of developing secondary calcification.

The frontal shield develops a variable number of foramina in the calcification. Foramina are smaller, but have essentially the same calcified structure and relationships as peristomes. They may be distributed all over the frontal shield or be confined to an area of variable extent in the centre. They develop from uncalcified embayments among lobes of peripheral calcification, and are cut off and isolated as the lobes fuse progressively towards the centre of the shield (Fig. 2C). In some species, the cuticle is inserted at the edge of the foramina (e.g. in *E. magna*); in others, it is continuous across the face of the foramina (see Cook 1985: 46). The calcification surrounding the foramina is usually thin and smooth, but varies considerably among species and at different ontogenetic stages. Usually the edges of the foramina are thin and slightly upturned early in ontogeny. As the upper surface of the shield thickens, the foramina deepen and become surrounded by a rim of calcification. If the outer edges of the rim are thicker than the inner edges, the foramina appear as pits in the centre of a smooth disc of calcification. Where the foramina are scattered, the subsequent appearance is similar to that illustrated in *E. antillea* from the Gulf of California (Osburn 1950, pl. 10, fig. 9). If the foramina are more numerous, the edges of the discs abut, but do not fuse, resulting in an appearance like that figured in *E. antillea* from Chios (Hayward 1974, fig. 4C), in *E. antillea* from Ghana (Cook 1985, pl. 15B and fig. 38), in *E. prelucidioides* from the Eocene of South Carolina (Canu Bassler, 1920, pl. 68, fig. 1), in Miocene *E. marginata* from Muddy Creek, Victoria (Fig. 6D), and Recent *Exechonella papillata* sp. nov. from southern Australia (Fig. 1B). If the foramina are infrequent, and their rims are curved, their appearance resembles that figured for *E. brasiliensis* from Brazil (Canu & Bassler 1928 pl. 3, fig. 5), from Komodo Island (Winston & Heimberg 1986, figs 26, 27), and from Vanuatu (Tilbrook *et al* 2001, fig. 8G). If the foramina are more numerous, their rims abut, and appear similar to those figured in *E. antillea* from Jamaica (Winston 1982, fig. 60), and *E. orbifera* (Canu & Bassler 1920, pl. 14, fig. 16) and *E. laticella* (Canu & Bassler 1920, pl. 55, fig. 6) from the Eocene of Alabama and North Carolina respectively. Although the foramina of species such as *E. papillata* sp. nov. and *E.* cf. *discoidea* appear to be open on the basal, exterior wall surface, it is inferred that the cuticular layer which lines the wall, is complete The cuticle investing the hypostegal coelom inserts sporadically on the outer edge of each foramen, and is raised above it in life. Preserved specimens show a cuticular layer covering the foraminal opening, and often in dried material, shrinking into the upper part of the foramen (Fig. 4C), as observed in *E. antillea* by Cook (1985: 46). This type of foramen appears to occur in Group 1 and Group 3 species, but not in *E. magna* (Group 2), where the foramina are completely open (Fig. 2B). A thin intervening coelom is presumed to surround the edges of the foramina and to remain in contact with the visceral coelom through the frontal marginal septular pores. Sometimes a cuticular trace surrounds a group of foramina, often giving a superficial appearance of a costate shield (Fig. 1B, and Cook 1985, pl. 15B). There is no simple correlation between form and frequency of the foramina and the number and position of septular pores. A single, very prominent, marginal series is present in several populations of *E. magna*, but the foramina do not develop much further, after the initial ontogenetic stages, and the calcification around them is smooth and not greatly thickened. In contrast, in *E. tuberculata*, the pores are fewer and obscured, but the foramina are marginally raised in irregular spinous processes, and the intervening calcification is thick and granular.

Opercula with marginal sclerites have been reported in *E. antillea* by Cook (1985), and Fransen (1986), and are present in *Exechonella papillata* sp. nov. and some, but not all populations of *E. magna* from southern Australia (see below). Fransen (1986) considered that the opercula were attached to the condyles, but Cook (1967), who observed living specimens of the same nominal species, noted that they were closely apposed to the calcified orifice, but were drawn downwards, together with the frontal mem-

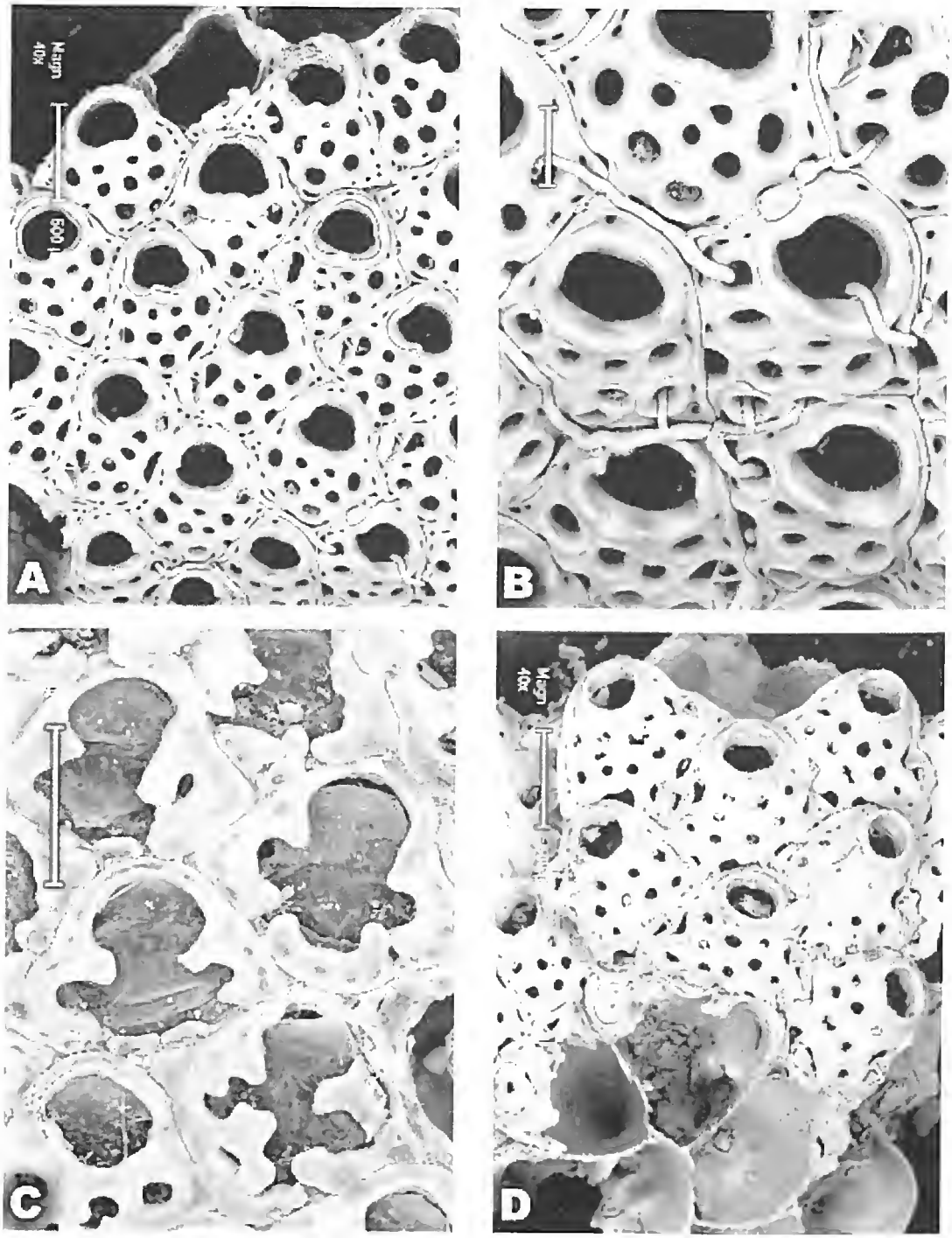


Fig. 2. A-D, *Exechonella magna* (MacGillivray 1895). A, B. GAB Station 103. A. Zooids with orifices showing proximal peristomial processes, avicularia with associated foramina, x28. B. Detail showing tubes of commensal organisms. Avicularia at top right and bottom centre, x57. C. GAB Station 134. Colony air-dried to show frontal membrane and operculum beneath incompletely calcified frontal shield, x47. D. Miocene, Muddy Creek. Central zooid with two avicularia, x28.

brane, almost to the basal wall, before opening, and protrusion of the tentacle sheath and crown (Cook 1985).

Small avicularia are frequently, but not invariably present. They are derived from a lateral, often oral, marginal frontal septular pore. Mandibles are slung on a delicate bar, and their shape is usually specifically correlated. Avicularia are generally very similar in material of each nominal species, but they are frequently absent from entire colonies, or parts of colonies. In the *E. magna* - complex, each avicularium is closely associated with a foramen, which may be larger than those occurring elsewhere in the shield. Structures which are not avicularia, but which have similar relationships with a foramen, occur in *Exechonella papillata* sp. nov. (see below).

Spines and ovicells are absent. Apart from the very doubtful and unillustrated record of ovicells in *E. discoidea* Canu & Bassler (1929, see below), they have not been reported in *Exechonella*. Cook (1985) described some enlarged, dimorphic, zooids in one specimen from west Africa referred to *E. antillea*. Fransen (1986) has illustrated the interior ovisac and brooding of embryos in non-dimorphic zooids of *E. antillea* sensu stricto.

NOTES ON AUSTRALIAN SPECIES OF *EXECHONELLA*

Exechonella Duvergier, 1924

Type species. Cyclicopora? grandis Duvergier, 1921.

Group 1. **Exechonella papillata** sp. nov.
(Figs 1A-D)

Holotype. NMV F97951 (figured specimen). Great Australian Bight. GAB Station 110, south of Esperance, Lat. 34°32' S, Long. 121°32' E, 154 m.

Paratype. NMV F97952 as above, large, multilaminar colony, originally encrusting shells, totalling 2500 zooids.

Other material. NMV GAB Station 089, southeast of Esperance, WA, Lat. 34°37' S, Long. 123°32' E, 210 m., single colony encrusting cemented sand, about 100 zooids.

Etymology. papilla (L), a nipple, referring to the small kenozooids.

Diagnosis. Exechonella with low peristomes and numerous frontal foramina; zooids each with one or two lateral kenozooids associated with a small foramen.

Description. Colony encrusting, unilaminar to multilaminar, with overgrowths in random directions. Zooids large, defined by a raised laminar border surrounding a series of small, marginal frontal septular pores. Lateral interzooidal communication by numerous pores scattered over the entire vertical walls. In a few zooids, a pair of small multiporous pore-plates also occur near the frontal edge of the walls, particularly, but not exclusively, on the distal walls. Their position is not correlated with that of the kenozooids (see below). Calcified orifice subrounded, tending to angular at proximal margin, length and width subequal; with a sharply delineated, smooth, slightly thickened peristomial rim. Operculum closely apposed to orifice, with well-marked lateral selerites. A pair of "condyles" within the calcified orifice are apparently associated with a distal lamina lining the peristome (see Fig. 1B). Each zooid has up to 80 small, rounded frontal foramina, surrounded by a disc of smooth calcification. In one or both lateral "corners" of many zooids, a small, round, kenozooidal structure is derived from a septular pore. It is not an avicularium, but is slightly raised, with an occluded, nipple-like region, which has a small central pore. Some of these structures have an oval, raised margin, which closely resembles an avicularian rostrum. However, none of these show any sign of a bar or a mandible. Nearly all these kenozooids have a small foramen within the raised rim of calcification, placed laterally to the central structure (Fig. 1D). Although very different in appearance, the relationship of the structure with the foramen is the same as in avicularia of *Exechonella magna* (see below).

Dimensions. Lz 0.45-0.59 mm, lz 0.43-0.50 mm, Lap (for secondary calcified orifice) 0.24-0.26 mm, lap 0.28-0.31 mm.

Remarks. This species does not appear to have been described before. It closely resembles some descriptions of specimens assigned to the "*E. antillea*"-complex, but differs completely in the much larger number of frontal foramina, and the occurrence of the small, lateral kenozooidal structures. The large colonies have allowed the investigation of the structure and ontogeny of the frontal shield in some detail.

Distribution. Known from the type and one other

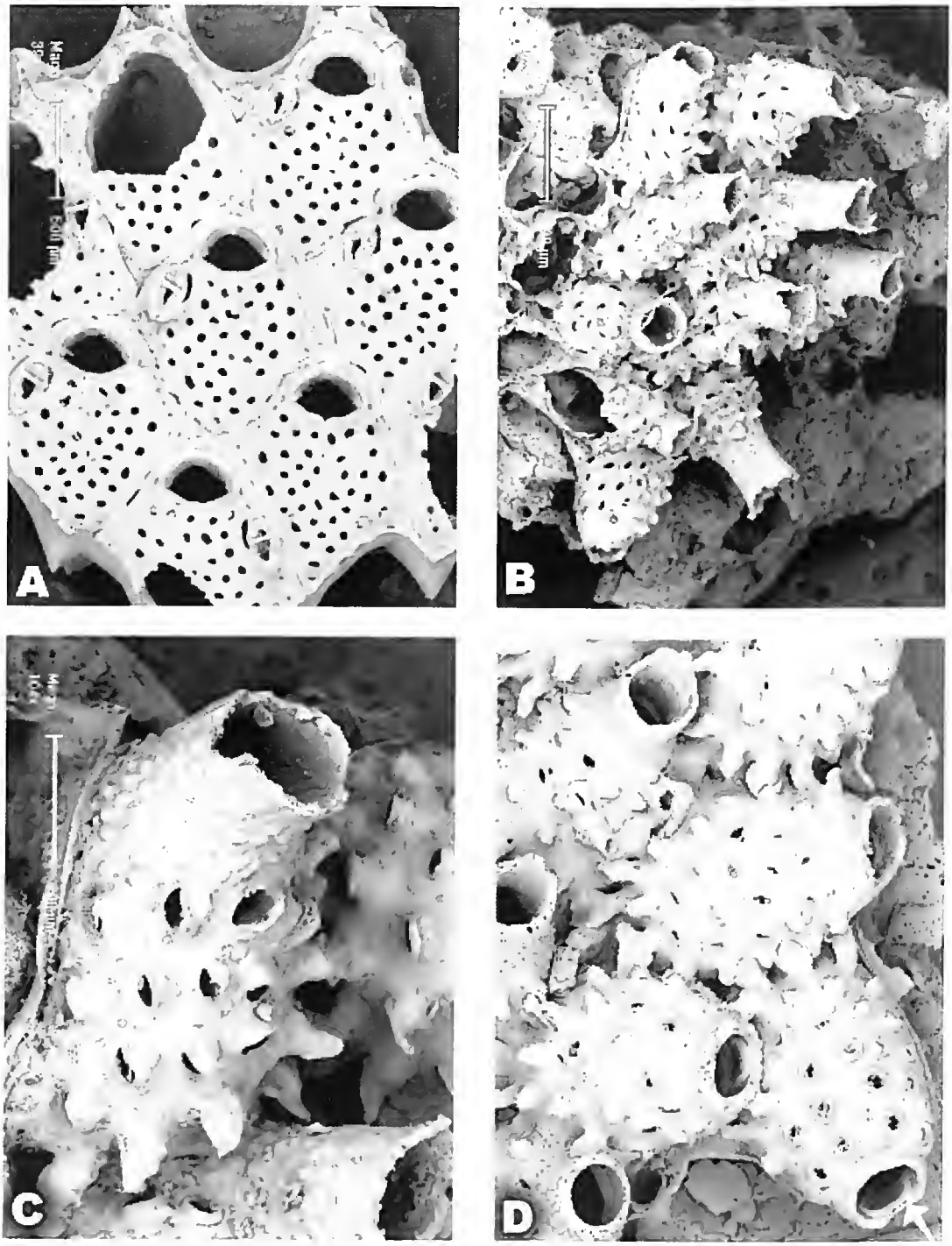


Fig. 3. A. *Exechonella magna* (MacGillivray 1895). Miocene, Balcombe Bay. Zooids with avicularia and about 30-40 small foramina, x29. B-D. *Exechonella tuberculata* (MacGillivray, 1883). Tangaroa 162. B. Small colony, showing tubular peristomes, and frontal foramina with raised, spinous marginal processes, x29. C. Single zooid, showing raised processes at edge of foramina, x95. D. Group of zooids. Note interzooidal fusion of some processes. Arrow shows "pockets" in orifice, x50.

loeality, off southwestern Australia.

Group 2. **Exechonella magna** (MacGillivray 1895).
(Figs 2A-D, 3A)

Hiantopora magna MacGillivray 1895: 62, pl. 8, fig. 23, pl. 10, fig. 27.
Exechonella magna. Wass & Yoo 1983: 331, Fig. 1.
Exechonella paucipunctata Brown 1956: 600, Fig. 1.

Lectotype. NMV P27645, selected here, figured by MacGillivray 1895, pl. 8, fig. 2, Muddy Creek, Miocene, Victoria.

Paralectotype. NMV P27697, selected here, figured by MacGillivray 1895, pl. 10, fig. 27, Muddy Creek, Miocene, Victoria.

Other specimens. NMV. Miocene. Two encrusting, worn fragments, totalling 100 zooids, Muddy Creek, Victoria. Two unilaminar fragments totalling seven zooids, Bairnsdale, Victoria. Six bilaminar fragments, totalling 200 zooids, Baleombe Bay, Victoria

Recent specimens from the Great Australian Bight (see appendix p. 00 for details). GAB Station 054, young colony on adeonid fragment, 16 zooids with growing edge and opereula. GAB Station 055, unilaminar fragment of 100 zooids. GAB Station 103, encrusting calcareous accretions with *Arachnopusia*, 200 zooids. GAB Station 105, young, ancestrulate colony encrusting massive "celleporid" with other species, 60 zooids. GAB Station 114, large bilaminar colony fragment, approximately 2000 zooids. GAB Station 134, four specimens, two encrusting small shell fragments and one unilaminar piece, each with 200 zooids, with one, ancestrulate, free-living "lunulitiform" colony with no substratum or means of attachment, 50 zooids. GAB Station 139, two unilaminar fragments, totalling 1000 zooids. NMV 46836 (Marine Biology section), Port Phillip Heads, Victoria, three unilaminar fragments totalling approximately 160 zooids.

Description. Colonies usually encrusting, or with unilaminar expansions; zooids wide, lozenge-shaped, rather flat, outlined by a slightly raised border, with a variable number of small, frontal, marginal septular pores, which sometimes occur on the distal side of the calcified orifice. Calcified orifice rounded with straight to curved proximal margin, width greater than length; with a thin distal lamina, but generally without "condyles", sometimes with raised proximal prominence. Operculum closely apposed to the calcified orifice; frontal membrane visible through the foramina. Frontal shield typically with from five to ten large, rounded foramina, but specimens with three, or up to 40 foramina known. Avicularia sporadic, lateral, acute, with a bar, flanked by a foramen, mandible elongated, orientated proximally.

Dimensions. Lz 0.75-0.96 mm, lz 0.64-0.78 mm, Lap (for secondary calcified orifice) 0.20-0.23 mm, lap 0.28-0.33 mm.

Remarks. Zooid size shows little variation within this species. However, other zooid characters such as number of foramina, varies considerably across populations, although within-colony variation is low. Zooids are defined by a shallow ridge and bordered by a series of small, marginal septular pores, which are sometimes numerous and well marked (Fig. 2A). Zooids are very deep, and communicate laterally by numerous uniporous septular pores. Unlike zooids of *Exechonella papillata* sp. nov., there seem to be no additional, multiporous pore plates. The calcified orifice is large, rounded, usually without "condyles", and slightly raised distally. In some material, there are small proximal or lateral processes on the edge of the shallow peristome, as in the specimen from GAB Station 103 (Fig. 2A). The colonies from GAB Station 134 exhibit a wide range of astogenetic and ontogenetic stages. One small, complete ancestrulate colony has no obvious substratum, and has developed a lunulitiform structure, with no apparent method of attachment. Another, virtually free-living, colony shows a number of zooids with partially calcified frontal shields (Fig. 2C). Although it appears probable that this is a reaction to a microenviron-mental influence, it does show the essential stages in frontal shield development. The apposed opereula and visible frontal membranes are a prominent feature of this specimen. Intraspecific variation is most obvious in characters of the frontal shields. In the fossil type specimens the shields have a range of 12-16 somewhat worn and irregular frontal foramina, and worn avicularia are present in a very few zooids. The supplementary, encrusting specimens from Muddy Creek resemble the type fragments closely, although they have a lower number (8-12) of foramina. One zooid has two avicularia (Fig. 2D). This is a very rare occurrence, but a similar zooid was figured in a population referred to *E. magna* from the Philippines by Canu & Bassler (1929, pl. 19, figs 1-2). The number of fo-

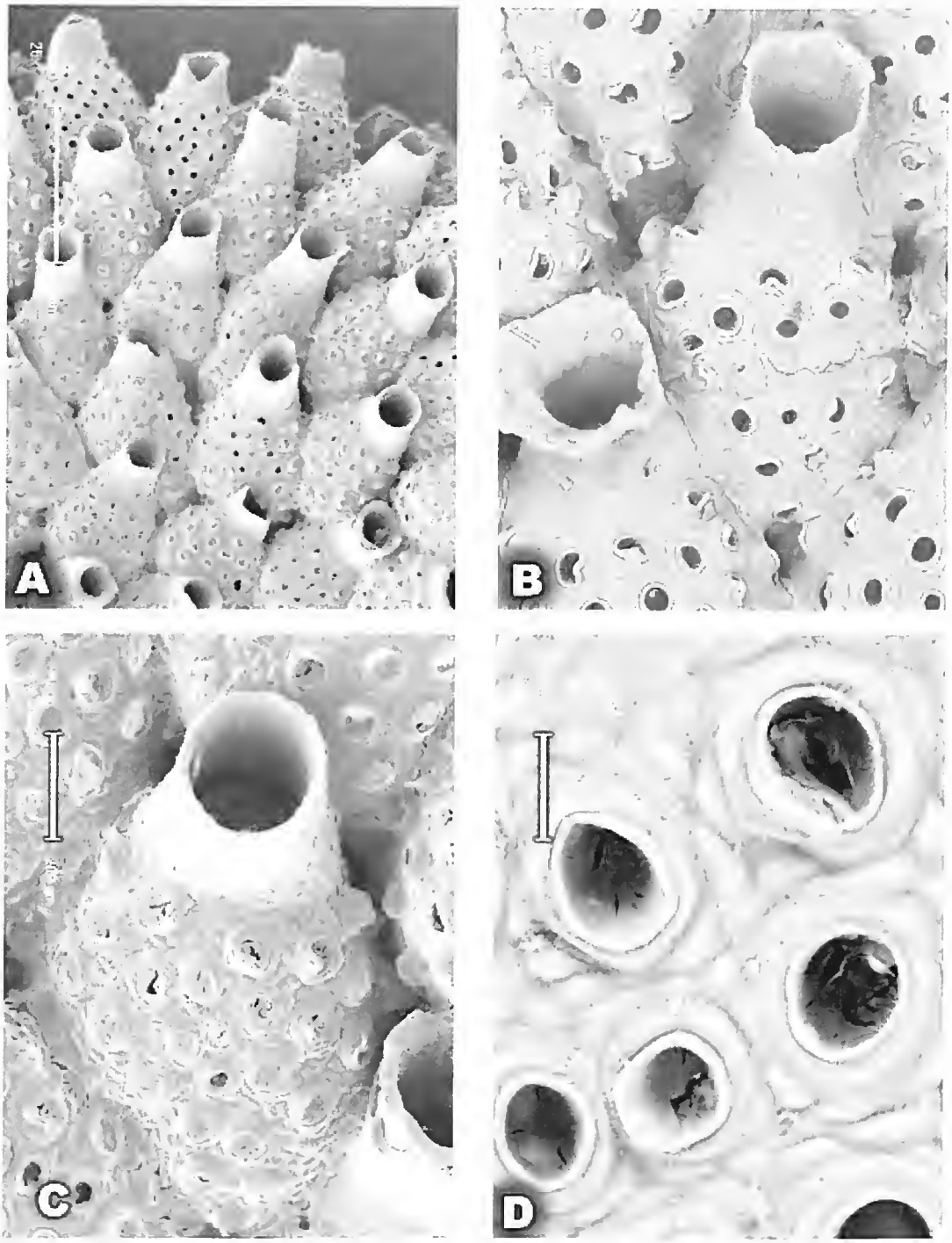


Fig. 4. A-D. *Exechonella* sp. cf. *discoidea* Canu & Bassler, 1929. GAB Station 119. A. Part of colony, air-dried, showing tubular peristomes, secondary electron image, x24. B. Detail of two zooid showing frontal calcification, back-scattered electron image, x65. C. Single zooid, secondary electron image to show cuticular cover of foramina, x78. D. Detail of foramina showing cuticular cover and calcified rim, back-scattered electron image, x310.

ramina in the unilaminar and encrusting specimens from Muddy Creek and Bairnsdale is in complete contrast to those in the zooids of the large, well preserved, bilaminar fossil specimens from Balcombe Bay. These have paired orificial "condyles" formed by a calcified lining within the distal rim of the orifice, which is wide and less rounded than those of other specimens. The frontal shields have from 28 to 40 rather small foramina, and the zooids present an appearance very different from that of the other fossil and Recent specimens (Fig. 3A). It is probable that if additional specimens became available, with these consistently different sets of characters, they could be regarded as specifically distinct from *E. magna* sensu stricto. The Recent specimens from the Great Australian Bight, figured by Wass & Yoo (1983: 331, fig. 11), have a lower range of five to nine frontal foramina, and resemble those from GAB Station 139. None of these zooids appears to have "condyles", but some have a slightly convex proximal edge to the peristome. The encrusting specimens from GAB Station 103, like the large, bilaminar colony from GAB Station 114, have an average of ten foramina, and avicularia are rare (Fig. 2A). Opercula are generally not markedly thickened with selerites, or marginally flanged, as they are in some populations of the "*E. antillea*"- complex (Cook 1985, Fransen 1986). Thin marginal opercular selerites are present in the young colony from GAB Station 105, but are not obvious in the large colony from GAB Station 114. The frontal foramina all have a slightly raised and thickened rim, and their shape is directly correlated with their frequency. The numerous foramina in the fossil specimens from Balcombe Bay are regularly rounded, whereas those from GAB Station 139 are infrequent and irregular in size and shape. Specimens from the Pliocene of South Australia, described and illustrated by Brown (1956: 600, fig. 1) as *E. paucipunctata*, appear to represent an end-term in the range of variation of frontal foramina in the *E. magna* -complex. The zooids had only three to four large, irregular foramina, but most other characters do not differ greatly from specimens examined here. The large foramina of *E. magna* are open, as is obvious from the occurrence of commensal organisms of unknown relationships, producing thin calcified tubes which wind in and out of the foramina (Fig. 2B). The specimen illustrated was alive when collected, and the cuticular frontal membrane and other uncalcified tissue was removed using bleach before examination by SEM. Although it is not known if any other species possesses similarly open foramina, this appears to be an important distinction between *E. magna* and the other species described here. A slide in the Museum Victoria collection (old registration 46836) from Port Phillip Heads, presumably collected in the late 19th century, is similar to the material from the Great Australian Bight, especially GAB Station 103 (Fig. 2A,B).

Avicularia are similar in all specimens. They originate from a marginal septular pore and are small, elongated, and raised, orientated proximally, with a slightly hooked mandible slung on a bar. They are always flanked on the inner side by a foramen, which is often enlarged, but has the same relationships as the foramen bordering the kenozooid in *E. papillata* (see above).

Other records dubiously referred to *E. magna* are those of Canu & Bassler (1929; 121, pl. 19, figs 1-4) from shallow water in the southern Philippines, and of *Lepralia foraminigera* var. Kirkpatrick (1890: 16, 19), described briefly from the type specimen from the China Sea by Harmer (1957: 654, fig. 52). The material from the Philippines was encrusting, and had zooids with 10-15 foramina, prominent, thickened peristomes and paired avicularia. Harmer mentioned that the avicularian mandibles of Kirkpatrick's specimen were setiform and projected beyond the rostrum terminally. These two populations are therefore probably not conspecific with *E. magna* sensu stricto, although they are certainly very similar in several characteristics to the specimens described here, and with them form a species-complex which has been present in the Australian region from the Miocene to the Recent.

Group 3. **Exechonella tuberculata** (MacGillivray, 1883).
(Figs 3B-D)

Lagenipora tuberculata MacGillivray 1883: 132, pl. 3, fig. 15.— MacGillivray 1888: 209, pl. 156, figs 1, 2.

Material examined. Holotype, NMV F45627, MacGillivray collection, Port Phillip Heads, Victoria. Additional specimens from Bass Strait Survey, "Tangaroa" Station 162, three ancestrulate colonies on small shells with 15 other species, totalling 60 zooids; BSS "Tangaroa" Station 155, ancestrulate colony on shell with two other species, totalling 70 zooids.

Description. Colonies small and encrusting, with large

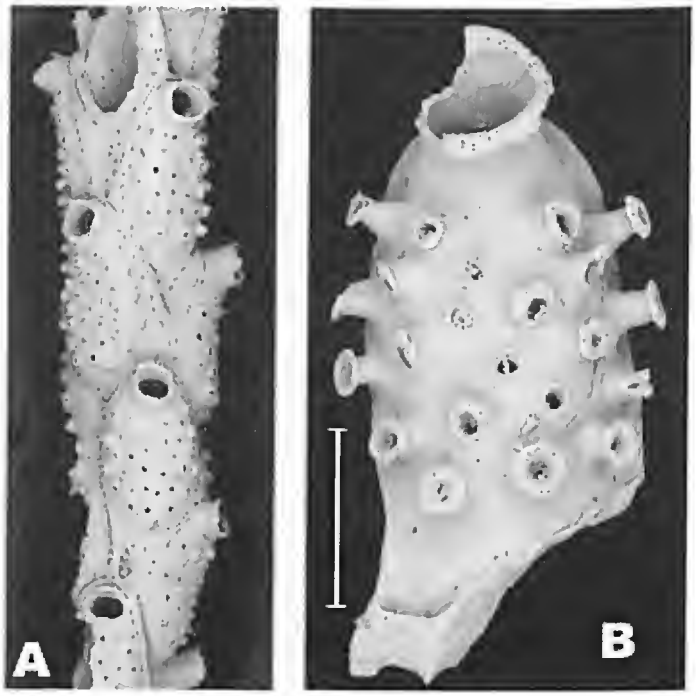


Fig. 5. A-B. *Exechonella marginata* (MacGillivray, 1895). Miocene, Balcombe Bay. Part of an erect branch, showing zooids with raised peristomes and foramina, x18. B. Zooid showing raised peristome, long, tubular frontal foramina, and proximal septular pores, x45.

zooids, although those of the ancestrular region are small. Zooids communicate laterally through one or two series of very small pores. The peristomes are long and tubular, but are often semi-repent and not prominent. The calcified orifice has a distal lamina which forms a pair of pockets, resembling occlusor laminae, at the base of the peristome (Fig. 3D), but "condyles" seem to be absent. The frontal shield is prominent and swollen, obscuring a single series of minute marginal septular pores within the limits of a very shallow interzooidal lamina. The number of foramina is rarely more than 20. They are circular very early in ontogeny, but rapidly become partially obscured, and are raised, often unilaterally, to form long, irregular, spinous processes which may fuse with those of neighbouring frontal shields. There are no avicularia.

Dimensions. Lz about 0.95 mm (excluding peristome), lz about 0.63 mm.

Remarks. The type specimen resembles MacGillivray's figures (1883: 132, pl. 3, fig. 15 and 1888: 209, pl. 156, figs 1, 2) closely. Although there are many records of this species, from an extensive geographical range, there are few illustrations of *E. tuberculata,* other than those of MacGillivray. The species has been reported from a wide range of localities extending from the Red Sea (Dumont 1981), through the Indian Ocean to the Philippines and East Indies (Harmer 1957), the specimens included here are those from the Port Phillip and Bass Strait area only. Although it is possible that they are conspecific with the other specimens described below (see *E.* cf. *discoidea*), they do differ in details of the calcified orifice and the development of frontal foramina.

Exechonella sp. cf. **discoidea** Canu & Bassler, 1929
(Figs 4A-D)

?*Exechonella discoidea* Canu & Bassler 1929: 123, pl. 20, figs 5, 6
?*Exechonella ampullacea* Hayward & Ryland 1995: 543, fig. 7E
?*Exechonella tuberculata* Gordon 1984: 70, Pl. 23D, not MacGillivray 1883, see above.

Material examined. Great Australian Bight, GAB Station 119, one colony, on other bryozoans, 50 zooids. GAB Station 065, two colonies, one ancestrulate colony, on shell, totalling 50 zooids. GAB Station 134, two small colonies encrusting large, calcareous ac-

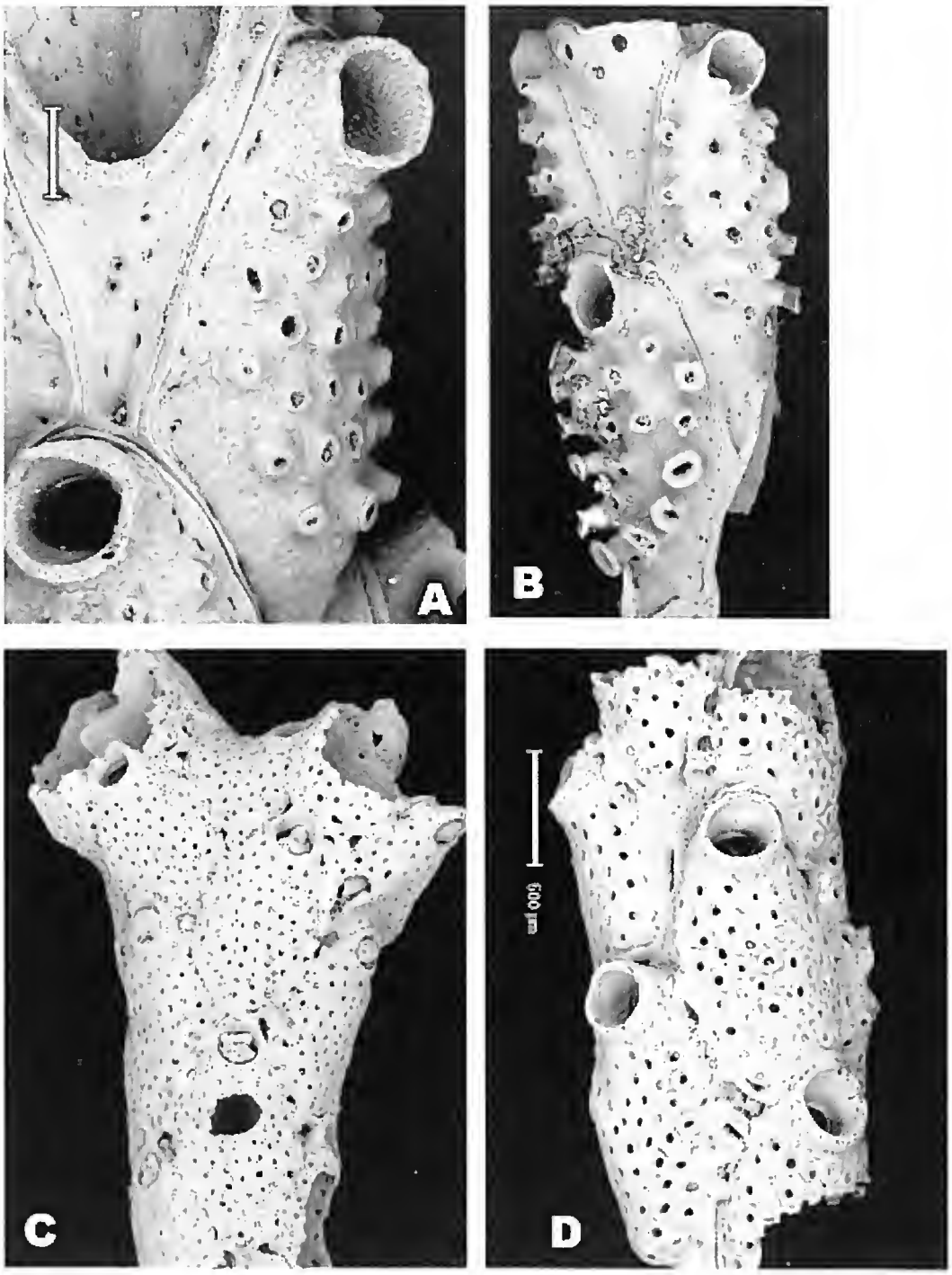


Fig. 6. A-D. *Exechonella marginata* (MacGillivray, 1895). A-B. Miocene, Balcombe Bay. A. Zooid showing tubular peristome and raised frontal foramina. Note the proximal grouping of frontal septular pores on zooid to left, x65. B. Group of three zooids showing long, tubular frontal foramina, x30. C-D. Miocene, Muddy Creek. C. Part of colony with branch bifurcation, x23. D. Detail of another colony, with zooids showing frontal calcification, and processes crossing zooids, x34.

eretion, totalling 50 zooids. GAB Station 139, colony on shell accretion, totalling 120 zooids.

Description. Colony encrusting, zooids small early in astogeny, later up to 1.3 mm in length, flask-shaped, with raised, tubular peristomes. Frontal foramina up to 25, slightly irregular and raised marginally. Calcified orifice apparently without distal lamina or "condyles", shallow, curved proximally. Marginal septular pores small, placed near the basal part of the lateral curvature of the frontal wall; no lamina apparent between zooids. Avicularia absent.

Remarks. The specimens, which are all from the western part of the Great Australian Bight, from 40-150 m depth, most resemble those reported by Gordon (1984) as *E. tuberculata*, from the Kermadec Ridge region, north of New Zealand, from 40-130 m depth. They have a similar flask-like shape, with long, tubular peristome, and a similar range in zooid length (approximately 0.9-1.4 mm), and number of frontal foramina (average 25).

The slightly irregularly-shaped foramina are raised marginally, and are surrounded by mamillate calcification, in contrast to the discs of smooth calcification surrounding the foramina in *E. papillata* sp. nov. In untreated specimens, the dried cuticle is seen stretched across the top of the raised foramen margin (Fig. 4C).

E. discoidea Canu & Bassler (1929) from Mindanao in the Philippines, from approximately 70 m depth, also shares some characteristics. The colonies were very small, and probably astogenetically young. The figured zooids are generally less than 1 mm in length. The zooids have long, somewhat irregular peristomes, and the number of foramina averages 15. The specimens named *E. tuberculata* from "Siboga" Station 164 (west end of New Guinea, 32 m), include two species, one of which has flask-like zooids less than 1 mm in length, with long tubular peristomes, and 15-19 foramina (see Harmer 1957, pl. 54, fig. 14). This appears to be very close to *E. discoidea*. Harmer (1957) also included another Philippine species, *Coleopora crinacea* Canu & Bassler (1929: 268, pl. 19, figs 6-8). This certainly belongs to *Exechonella* (see Harmer 1957: 653, footnote), not *Coleopora*. Some, but not all, of Canu & Bassler's illustrations (for example pl. 19, fig. 7), also appear to be close to *E. discoidea* , but without examination of further specimens, it is not possible to determine their identity. *E. discoidea* was originally described as having ovicells, but these were not illustrated. Another, somewhat similar species, *E. ampullacea*, with raised, tubular peristomes, but smaller zooids (0.7-0.9 mm), with more numerous, rounded foramina (up to 40), was described from shallow water from the Great Barrier Reef by Hayward & Ryland (1995: 547, fig. 7E). It somewhat resembles both *E. discoidea* and the specimen from the Kermadec region illustrated as *E. tuberculata* by Gordon (1984).

Group 4. **Exechonella marginata** (MacGillivray, 1895).
(Figs 5A, B, 6A-D)

Tubucellaria marginata MacGillivray 1895: 105, pl. 4, figs 2, 3.— Maplestone 1904: 214.

Type material. NMV P27553, figured by MacGillivray 1895, pl. 4, figs 2, 2a, 2b, Muddy Creek, Victoria (Population 1). NMV P 27554, figured by MacGillivray 1895, pl. 4, fig. 3, Schnapper Point, Victoria (Population 2).

Other material examined. Population 1. Muddy Creek, Victoria, nine quadriserial fragments, totalling 65 zooids. Griees Creek, Victoria, five fragments, totalling 55 zooids. Population 2. Balcombe Bay, Victoria, 15 fragments, totalling 65 zooids. Batesford Quarry, Victoria, 7 fragments totalling 17 complete zooids. Bairnsdale, Victoria, 5 fragments totalling 12 zooids. Population 3. Cooriemungle, 10 fragments, totalling 25 zooids. Balcombe Bay, 11 fragments, totalling 37 zooids.

Description. Colony erect, branching; branches cylindrical, nearly all quadriserial, with one from Muddy Creek showing a dichotomous branch. Zooids elongated, defined by a raised rim of calcification, bordering a marginal series of septular pores. Laterally, the zooids communicate by one or two series of scattered pores. Calcified orifice almost circular, lacking "condyles", peristome often very raised and tubular, sometimes flaring terminally. Frontal shield includes a very variable number of rounded foramina, each with a raised rim. Avicularia absent.

Dimensions. Lz about 1.4 mm, lz about 0.68 mm. Lap (secondary orifice) about 0.26mm, lap about 0.27mm.

Remarks. MacGillivray (1895: 105) referred this species to the genus *Tubucellaria* d'Orbigny, 1852. It was listed by Maplestone (1904: 214) from several other Tertiary Victorian localities. MacGillivray's (1895) figures illustrate two of the populations exhibiting part

of the range of variation. In the Population 1 zooids illustrated in Figures 2, 2a and 2b, and the specimens from Muddy Creek and Griees Creek examined here, there are 50-60 closely spaced foramina with rounded, but not greatly raised margins. The hypostegal coelom appears to develop extrazooidal lobes of calcification, which extend above the zooidal margins and septular pores, and fuse with lobes from neighbouring zooids, leaving a series of irregular embayments (Fig. 6C, D). This extrazooidal calcification is present in all specimens examined, and, in fact, was illustrated by MacGillivray in Pl. 4, fig. 2a, at the proximal end of the fragment. Zooids from Population 2 were illustrated by MacGillivray in Pl. 4, fig. 3, from a specimen from Schnapper Point. Specimens from Bairnsdale, Batesford Quarry and Balcombe Bay resemble these figures in having more prominent peristomes, and zooids with from 30-40 frontal foramina, which are more widely spaced, and often raised marginally (Fig. 5A, 6A). The branch fragments and the zooids of Populations 1 and 2 are generally not as robust as those of Population 3 (Fig. 5B, 6B). The zooids from Cooriemungle and Balcombe Bay, belonging to this population, are very large and defined by a distinctly raised rim. There is a series of marginal septular pores, which may be grouped in an extensive, depressed area of proximal frontal shield which has no foramina. The peristome is raised, tubular and often prominent. The most noticeable difference in these zooids is in the number of frontal foramina, which rarely exceed 24, and may be as low as 12. The foramina are confined to an area in the central part of the frontal shield, and the calcification surrounding them is smooth. Most foramina are raised and tubular, some equalling the peristome in length, and nearly all flaring terminally. There is no development of extrazooidal bridges of calcification between zooids, as in the zooids of Population 1.

Although the specimens examined fall fairly clearly into three population groups, the form of the foraminal calcification is correlated with frequency, as it is in *E. magna*. Only investigation of much larger samples of each morphotype would show whether there were two or more distinct taxa present or not. The inner surface of the tubular foramina is part of the exterior wall forming the basal side of the shield, and has no connection with the visceral coelom. The area frontal to the upper, interior-walled part of the shield is inferred to have been occupied by hypostegal coelom bounded by cuticle, presumably carried up frontally and surrounding the tubular foramina. Although the foramina of *E. tuberculata* develop in a somewhat similar way, they are not as extensive. Harmer (1957: 653) included *T. marginata* in the synonymy of *Exechonella tuberculata*. It differs in colony form, in the relationships of the marginal septular pores to the rest of the frontal shield, and in the form of the frontal foramina. It also differs in the absence of internal "pockets" at the base of the peristome.

Relationships. The development of a considerably more extensive secondary and tertiary frontal shield, derived from a hypostegal coelom, occurs in another genus which has been referred to the Exechonellidae. This is *Stephanopora* Kirkpatrick, described in detail by Hayward (1988) and by Gordon (1993). In *S. cribrispinata* Kirkpatrick, the tubular expansions of foramina are raised as in *E. marginata* Population 3, but fuse with each other terminally. They form a porous, secondary shield composed of exterior wall, derived from the lower surface of the umbonuloid primary shield. The hypostegal coelom remains to form a labyrinthine intervening layer at a lower level. Hollow spinous outgrowths from the peristome then fuse interzooidally, forming a tertiary shield. In another species of *Stephanopora*, *S. perelegans*, the flattened, "semi-spinous" processes derived from the peristome, have a structure exactly like that of an umbonuloid wall, namely, their basal side is exterior, but the frontal side is an interior wall covered by an extension of hypostegal coelom and bounded by a cuticle. This type of development is remarkably similar to that described in the Cretaceous arachnopusiid genus *Ramicosticella* by Voigt & Gordon (1998). The type species, *R. erratica*, from the Danian of Germany, produces the equivalent of an umbonuloid shield from pairs of branched, flattened semi-spines which originate at the proximal end of the zooid, from paired septular pores, and spread interzooidally over the zooid frontals, fusing irregularly. Voigt & Gordon (1998) discounted this form of development as a possible indication of an origin of some umbonuloid walls, from "cribrilinid" ancestors which were uncalcified frontally. There is, admittedly, no earlier fossil evidence for a linking form or forms, but this type of origin remains feasible, as it requires no more than the control of calcification at specific sites, which is inherent in the Bryozoa in general, and is expressed in a random and mosaic manner. The different kinds and degrees of distribution and development of hypostegal coeloms in the Exechonellidae suggests that there were almost certainly more methods of producing frontal shields than have at present been established.

ACKNOWLEDGEMENTS

We should like to thank Dr. Yvonne Bone (University of Adelaide) and the Master and crew of C.S.I.R.O. MV "Franklin" for the opportunity for one of us (P.E.B.) to participate in the program which collected material from the Great Australian Bight in July 1995. Chris Rowley, Dr David Holloway, and Dr Rolf Schmidt have kindly made specimens from the Museum of Victoria collections. An earlier version of this paper was read at the 2001 Dublin Conference of the International Bryozoology Association.

APPENDIX
LOCALITIES MENTIONED IN THE TEXT

Tertiary of Victoria.

Bairnsdale. Approximately 12 km west of Bairnsdale. Lat.37°47.9'S, Long.147°29.5'E.
Age: Miocene.

Balcombe Bay and possibly Schnapper Point. On the coast of Port Phillip Bay,
approximately 3 km south of Mornington. Lat.38°14.5'S, 145°01.7'E. Fyansford Clay. Age: Baleombian, Middle Miocene (Langhian).

Batesford Quarry. Upper levels of limestone quarry, 7 km west of Geelong. Lat. 38°06.5'S, Long. 144°17.3'E. Fyansford Clay. Age: Balcombian, Middle Miocene
(Langhian).

Cooriemungle. Road cuttings approximately 18 km north of Princetown. Lat. 38°32.4'S,
Long. 143°08.1'E. Gellibrand Marl. Age: Balcombian, Middle Miocene.

Grices Creek. On the coast of Port Phillip Bay, approximately 8 km north of Mornington. Lat. 38°11.9'S, Long. 145°03.9'E. Fyansford Clay. Age: Baleombian (some material may be Bairnsdalian), Middle Miocene.

Muddy Creek. Clifton Bank, Muddy Creek, 8 km west of Hamilton. Lat. 37°44.6'S, Long. 141°56.4'E. Muddy Creek Marl (=Gellibrand Marl). Age: Baleombian, Middle Miocene.

R.V. Franklin cruise, July 1995, Great Australian Bight stations.

GAB054: N. E. of Esperanee. Lat. 33°12'S, Long. 124°55'E, 54 m.

GAB055: N. E. of Esperance. Lat. 33°16'S, Long. 125°18'E, 59.5 m.

GAB065: N. E. of Esperance. Lat. 33°03'S, Long. 124°23'E, 42.5 m.

GAB103: off Esperanec. Lat. 33°58'S, Long. 121°56'E, 55 m.

GAB105: SW of Esperancc. Lat. 34°04'S, Long. 121°44'E, 78 m.

GAB110: S. of Esperance. Lat. 34°32'S, Long. 121°32'E, 154 m.

GAB114: SW of Esperance. Lat. 34°37'S, Long. 121°32'E, 190 m.

GAB119: E of Albany. Lat. 35°S, Long. 119°E, 149 m.

GAB134: W of Cape Mentelle. Lat. 34°02'S, Long. 114°48'E, 51 m.

GAB139: W of Cape Naturaliste. Lat. 33°35'S, Long. 114°46'E, 49 m.

NMV Bass Strait Survey stations.

Tangaroa (BSS) 155: Lat. 38°34'S, Long. 144°54.3'E, 70 m

Tangaroa (BSS) 162: Lat. 39°46'S, Long. 146°18'E, 80 m.

REFERENCES

Brown, D. A., 1956. Some Pliocene Polyzoa from South Australia. *Annals and Magazine of Natural History* (12) 9: 593-611.

Busk, G., 1860. Zoophytology. Shetland Polyzoa. Collected hy Mr.Barlee (Continued and concluded). *Quarterly journal of microscopical science* 8: 213-214.

Canu, F. & Bassler, R. S., 1920. North American Tertiary Bryozoa. *Bulletin of the United States National Museum* 106: i-xx, 1-879.

Canu, F. & Bassler, R. S., 1923. North American later Tertiary and Quaternary Bryozoa. *United States National Museum Bulletin* 125: 1-302.

Canu, F. & Bassler, R. S., 1927. Classification of the cheilostomatous Bryozoa. *Proceedings of the U.S. National Museum* 69: 1-42.

Canu, F. & Bassler, R. S., 1928. Bryozoaires du Brésil. *Bulletin de la Société des Sciences de Seine-et-Oise* 9 (5): 58-100.

Canu, F. & Bassler, R. S., 1929. Bryozoa of the Philippine Region. *Bulletin of the United States National Museum* 100: v-ix, 1-685.

Cheetham, A. H., 1966. Cheilostomatous Polyzoa from the Upper Bracklesham Beds (Eocene) of Sussex. *Bulletin of the British Museum (Natural History) Geology* 13 (1): 1-115.

Cheetham, A. H. & Cook, P. L., 1983. General Features of the Class Gymnolaemata. In *Treatise on Invertebrate Paleontology, Part G, Bryozoa*

Revised, Boardman, R. S. et al., eds, The Geological Society of America, Inc. and the University of Kansas, Boulder, Colorado and Lawrence, Kansas, 138-207

Cook, P. L., 1967. Polyzoa (Bryozoa) from West Africa. The Pseudostega, the Cribrimorpha and some Ascophora Imperfecta. *Bulletin of the British Museum (Natural History) Zoology* 15 (7): 321-351.

Cook, P. L., 1985. Bryozoa from Ghana, a preliminary survey. *Annales des Musée Royal de l'Afrique Centrale, Tervuren, Belgique, sciences zoologiques* 238: 1-315.

Dumont, J. P. C., 1981. A report on the cheilostome Bryozoa of the Sudanese Red Sea. *Journal of natural history* 15: 623-637.

Duvergier, J., 1921. Note sur les Bryozoaires du Néogène de l'Aquitaine. *Actes de la Société linnéenne de Bordeaux* 72: 145-181.

Duvergier, J., 1924. Deuxiéme note sur les Bryozoaires du Néogène de l'Aquitaine. *Actes de la Société linnéenne de Bordeaux* 75: 145-190.

Fransen, C. H. J. M., 1986. Caribbean Bryozoa: Anasca and Ascophora Imperfecta of the inner bays of Curaçao and Bonaire. *Studies on the Fauna of Curaçao and other Caribbean Islands* 68: 3-119.

Gordon, D. P., 1984. The marine Fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *Memoirs. New Zealand Oceanographic Institute* 91: 1-198.

Gordon, D. P., 1993. Bryozoan frontal shields: studies on umbonulomorphs and impacts on classification. *Zoologica Scripta* 22 (2): 203-231.

Gordon, D. P. & d'Hondt, J.-L., 1997. Bryozoa: Lepraliomorpha and other Ascophorina from New Caledonian waters. *Mémoires du Muséum National d'Histoire Naturelle* 176, 9-124.

Harmer, S. F., 1957. The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora II. *Siboga-Expeditie* 28d: v-xv, 641-1147.

Hayward, P. J., 1974. Studies on the cheilostome bryozoan fauna of the Aegean Island of Chios. *Journal of Natural History* 8: 369-402.

Hayward, P. J., 1988. Mauritian cheilostome Bryozoa. *Journal of Zoology, London* 215: 269-356.

Hayward, P. J. & Ryland, J. S., 1995. Bryozoa from Heron Island, Great Barrier Reef. 2. *Memoirs of the Queensland Museum* 38 (2): 533-573.

Kirkpatrick, R., 1888. Polyzoa of Mauritius. *Annals and Magazine of Natural History* (6) 1, 72-85.

Kirkpatrick, R., 1890. Report on the Hydrozoa and Polyzoa collected by P.W.Bassett-Smith, Esq., Surgeon R.N., during the survey of the Tizard and Macclesfield Banks, in the China Sea, by H.M.S. 'Rambler', Commander W.U.Moore. *Annals and Magazine of Natural History* (6) 5: 11-24.

MacGillivray, P. H., 1883. Descriptions of New, or Little Known, Polyzoa. Part II. *Transactions and Proceedings of the Royal Society of Victoria* 19: 130-138.

MacGillivray, P. H., 1888. Polyzoa. In *Prodromus of the Zoology of Victoria, Decade XVI*, F. McCoy ed., Government Printer, Melbourne, 209-220.

MacGillivray, P. H., 1895. A monograph of the Tertiary Polyzoa of Victoria. *Transactions of the Royal Society of Victoria* n.s 4: 1-166.

Maplestone, C. M., 1904. Tabulated list of the fossil cheilostomatous Polyzoa in the Victorian Tertiary deposits. *Proceedings of the Royal Society of Victoria* n.s. 17: 182-219.

D'Orbigny, A., 1852. *Paléontologie française, Terrains Crétacés, V, Bryozoaires*. Victor Masson: Paris: 185bis-472.

Osburn, R. C., 1927. The Bryozoa of Curaçao. *Bijdragen tot de Dierkunde, Amsterdam* 25: 123-132.

Osburn, R. C., 1950. Bryozoa of the Pacific coast of America, Part 1. Cheilostomata - Anasca. *Report of the Allan Hancock Pacific Expeditions* 14 (1): 1-269.

Osburn, R. C., 1952. Bryozoa of the Pacific coast of America, part 2, Cheilostomata-Ascophora. *Report of the Allan Hancock Pacific Expeditions* 14: 271-611.

Poluzzi, A., 1977. Contributi per una revisione del genera *Tenchopora* Neviani 1895 (Bryozoa, Cheilostomata). *Bollettino della Società Paleontologica Italiana* 16: 69-77.

Smitt, F. A., 1868. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. IV. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 25: 3-230.

Smitt, F. A., 1873. Floridan Bryozoa collected by Count L.F. de Pourtales, Part 2. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 11: 1-83.

Tilbrook, K. J., Hayward, P. J. & Gordon, D. P., 2001. Cheilostomatous Bryozoa from Vanuatu. *Zoo-*

logical Journal of the Linnean Society 131 (1): 35-109.

VIGNEAUX, M., 1949. Révision des Bryozoaires néogènes du Bassin d'Aquitaine et essai de classification. *Mémoires de la Société Géologique de France, n.s.* 28: 1-153.

VOIGT, E. & GORDON, D. P., 1998. *Ramicosticella* gen. nov., a new Danian genus of Araehnopusiidae (Bryozoa, Cheilostomatida). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* n.f. 37: 95-104.

WASS, R. E. & YOO, J. J., 1983. Cheilostome Bryozoa from the Southern Australian Continental Shelf. *Australian Journal of Marine and Freshwater Research* 34: 303-354.

WINSTON, J. E., 1986. An Annotated Checklist of Coral-Associated Bryozoans. *American Museum Novitates* 2859: 1-39.

WINSTON, J. E. & HEIMBERG, B. F., 1986. Bryozoans from Bali, Lombok and Komodo. *American Museum Novitates* 2847: 1-49.

Manuscript received 22 December 2003
Revision accepted 21 July 2004

NEW SPECIES OF THE BRYOZOAN GENERA *BATOPORA* AND *LACRIMULA* (BATOPORIDAE) FROM AUSTRALIA

P. E. Bock[1] & P. L. Cook[2]

[1]School of Ecology and Environment, Deakin University, Melbourne Campus, Burwood Highway, Burwood, Victoria 3125. email pbock@deakin.edu.au
[2]Honorary Associate, Marine Biology Section, Museum of Victoria, GPO Box 666E, Melbourne, VIC 3001, Australia.

Bock, Philip E. & Cook, Patricia L. 2004:12:04. New species of the bryozoan genera *Batopora* and *Lacrimula* (Batoporidae) from Australia. *Proceedings of the Royal Society of Victoria* 116(2): 269-274. ISSN 0035-9211.

Examination of samples of bryozoans from the south- eastern slope sediments of Australia ("Franklin" SLOPE Stations 6, 7), has revealed the presence of many specimens of several genera with species which have minute, rooted colony forms. Among these are new species of the genera *Batopora* Reuss (*B. problematica*) and *Lacrimula* Cook (*L. affinis*). The structure of colonies is briefly described. The family Batoporidae is considered to contain only these two genera, although they have relationships with the discoidal genus *Orbitulipora*, and similarities in colony form to the genera assigned to the Conescharellinidae.

Keywords: Bryozoa, Cheilostomata, Batopoidae, *Lacrimula*, *Batopora*, Australia, new taxa

THE STRUCTURE and affinities of both *Batopora* and *Lacrimula* were described by Cook & Lagaaij (1976) in some detail. Copiously illustrated notes on the astogeny of *Batopora* have recently been provided by Pizzaferri & Braga (2000). Both genera include small, conical or globular (conescharelliniform) colonies, which are known from Recent examples, to be anchored by rootlets. Colonies are formed entirely by "reversed frontal budding", and in this respect are similar to species of both Conescharellinidae and the genus *Sphaeropora* (Lepraliellidae). However, the Batoporidae does not appear to be closely related to either of these groups.

Material and methods. All specimens are part of the collections of the Museum of Victoria (NMV), and were collected by the RV "Franklin" from two Stations: Stn 6 off Nowra NSW 34°51.90'S 151°12.60'E 770 m, 15.7.86, bottom, crinoid dominated, and Stn 7 off Nowra NSW 34°52.29'S 151° 15.02'E 1096 m, 15.7.86, epibenthic sled. All the colonies of *Batopora* and *Lacrimula* were accompanied by two species of *Trochosodon* and four species of *Conescharellina*.

Measurements. Lor, lor, length and width of orifice; Lov, lov, length and width of ovicell; Lav, lav, length and width of avicularian rostrum.

BATOPORIDAE Neviani, 1901

Batoporideae Neviani 1901: 220 (106).
Orbituliporidae Canu & Bassler 1923 part: Cook & Lagaaij 1976 part.
Batoporidae (presumably for Batoporideae) Gordon & d'Hondt 1997: 70.

Type genus. Batopora Reuss (1867)

Remarks. Batoporidae includes only *Batopora* and *Lacrimula*. Gordon & d'Hondt (1997) emended Neviani's name, and regarded it as a senior synonym of "Orbituliporidae" in general, but did not discuss which genera had been assigned to either family. Neviani (1901) included *Batopora* with *Conescharellina*, which last is referable to the family Conescharellinidae. Canu & Bassler (1923) included a wide range of genera, the majority of which has been assigned subsequently to other families.

Batopora and *Lacrimula* include a range of very similar forms. At present, the distinction between genera relies upon the differences in shape of primary orifice, in the origin of rootlets, and in the relationships of the ovicell. Orbituliporidae is maintained here for the discoidal genus *Orbitulipora*.

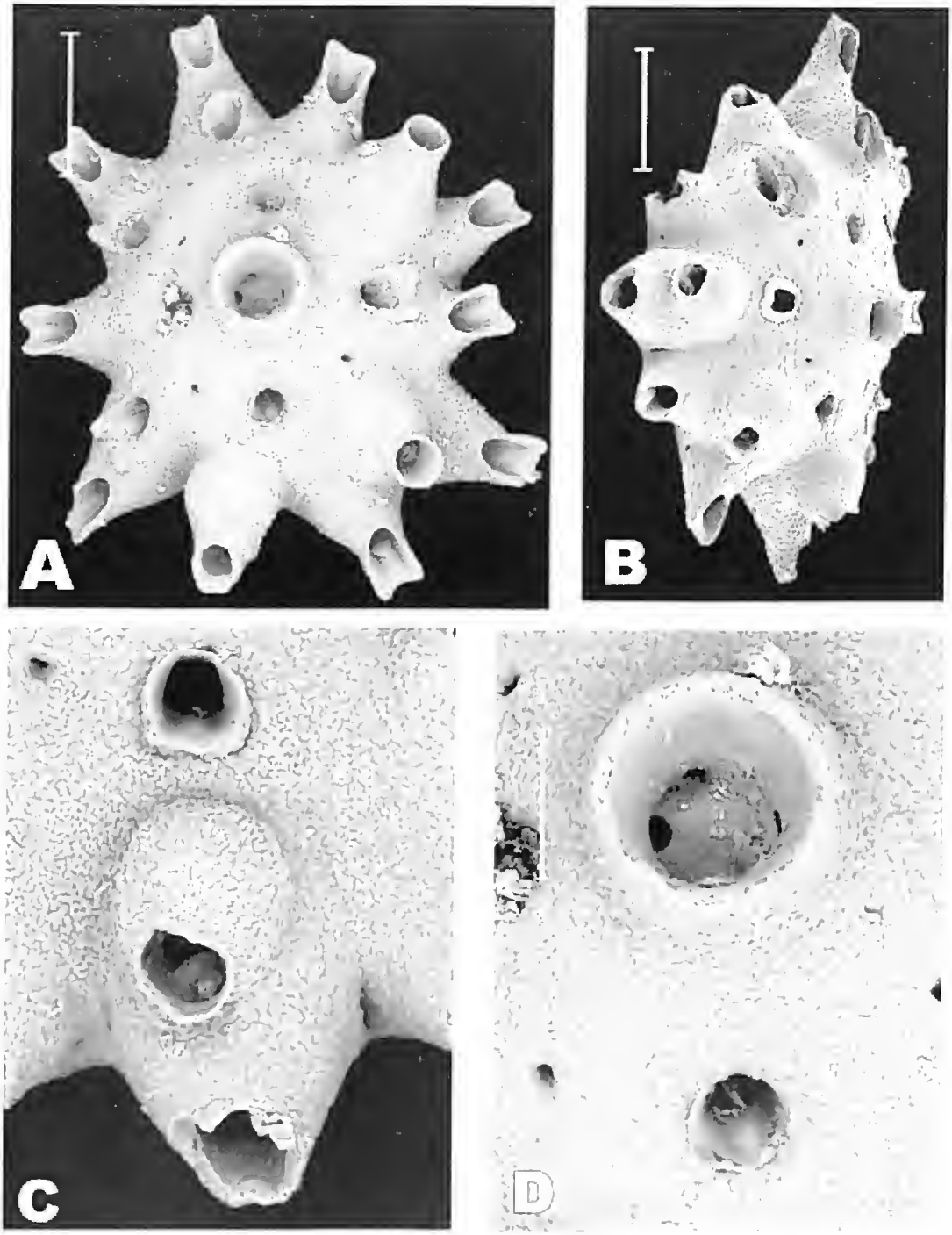


Fig. 1. A-D, *Batopora problematica* sp. nov. A, D. Holotype, NMV F98031. A. Colony, adapical view showing central kenozooid and two ovicells, x42. D. Central kenozooid showing cribrate plate, x110. B, C. Paratype, NMV F98032. B. Lateral view of colony with ovicells, x36. C. Detail of primary orifice and ovicell, x108.

Batopora Reuss 1867

Type species. B. stoliczkai Reuss 1867: 223. pl. 2, figs 2-4.

Description. Colonies usually small (up to 3 mm diameter in one species), globular or conical (conescharelliniform), all zooids originating from reversed frontal buds. Zooid orifices not sinuate, with a slightly curved antapical edge. Ovicells prominent, peristomial, not closed by the operculum. Avicularia small, interzoooidal, with paired condyles, or absent. Rootlets arising from an adapical pit, surrounded by kenozooids, or from a single, central, prominent adapical kenozooid. Recent species are from deep, or very deep water.

Remarks. The type species, from the Lower Oligocene of Germany, has very small globular colonies with minute interzooidal kenozooids. A better understanding of the characters of the species *B. stoliczkai*, and its relationship with *B. multiradiata* Reuss 1869, requires revision of the European material. The genus has a long fossil record extending from the Lower Eocene of Europe (Cook & Lagaaij 1976).

Gordon & d'Hondt (1997) have suggested that *Batopora* sensu lato almost certainly includes a diversity of species which may not be strictly congeneric. It is also obvious that the increasing diversity of known forms of *Lacrimula* Cook makes separation of the genera somewhat arbitrary, and we agree that both *Batopora* and *Lacrimula* require revision. Gordon & d'Hondt (1997) introduced a new genus group, *Ptoboroa*, for a previously named species, *Batopora pulchrior* Gordon (1989), from New Zealand, and added a new form, *P. gelasinus*, from New Caledonia. Both these species were illustrated with distinct adapical pores on the edge of the peristome. These pores are known to be the origin of ovicells in Conescharellinidae, the development of which was illustrated in *Conescharellina* by Gordon (1985, fig. 23) and in *P. pulchrior* by Gordon (1989, pl. 48A). The ovicells of *P. pulchrior* have an ectooecium and wide entooecial frontal area, and resemble those known in species of Conescharellinidae. The ovicells of *Batopora* and *Lacrimula* are peristomial and hyperstomial respectively, do not have an exposed entooecial area, and do not develop from an adapical pore. It appears therefore, that in spite of its central, cribrate rootlet kenozooid, which is almost exactly like that of *B. problematica*, *Ptoboroa pulchrior* is not a member of the Batoporidae, but is referable to a distinct genus of Conescharellinidae.

Batopora problematica sp. nov.
(Figs 1A-D, 2A)

Holotype. NMV F98031, figured specimen SLOPE Stn 7.

Paratype. NMV F98032, figured specimen. SLOPE Stn 7.

Other material. SLOPE Stn 7, 10 colonies, 9 with ovicells, 1 with rootlet. SLOPE Stn 6, 5 colonies, 4 with ovicells, 1 with rootlet.

Etymology. problema (Gr.), a puzzle, referring to the complex of morphological characters present.

Description. Colonies small, stellate, fairly flat, with an adapical central kenozooidal rootlet tube, which has a central cribrate plate. Zooids in whorls of 4-5; frontal calcification finely granular, mainly imperforate with rare marginal frontal septular pores. The zooids have elongated peristomes, which are extended antapically, concealing a primary orifice which is curved on the antapical side in an adapical direction. Ovicells, large, prominent, peristomial, not closed by the operculum, frontal calcification similar to zooids. Avicularia absent.

Remarks. B. problematica has far smaller colonies than *B. murrayi* Cook (1966) from the western Indian Ocean, but resembles *B. lagaaiji* and *B. nola* from eastern South Africa, described by Hayward & Cook (1979), and discussed by Cook (1981). These latter species have colonies that are similar in size to *B. problematica*, but are proportionally higher, with a smaller central, rootlet kenozooid. An unnamed species from a New Caledonian locality (without data), was figured by d'Hondt (1986, pl. 8, fig. 2), and appears to resemble *B. problematica*. Gordon (1989: 81) suggested that it might be placed in the same genus as *B. pulchrior*.

The strikingly similar appearance of *Batopora problematica* and the type species of *Ptoboroa* Gordon & d'Hondt (1997), *Batopora pulchrior* Gordon (1989), emphasizes the complexities of morphological characters and character states found among species and putative generic groups with conescharelliniform colonies. To a certain extent, this is a result of the constraints of minute size, reversed

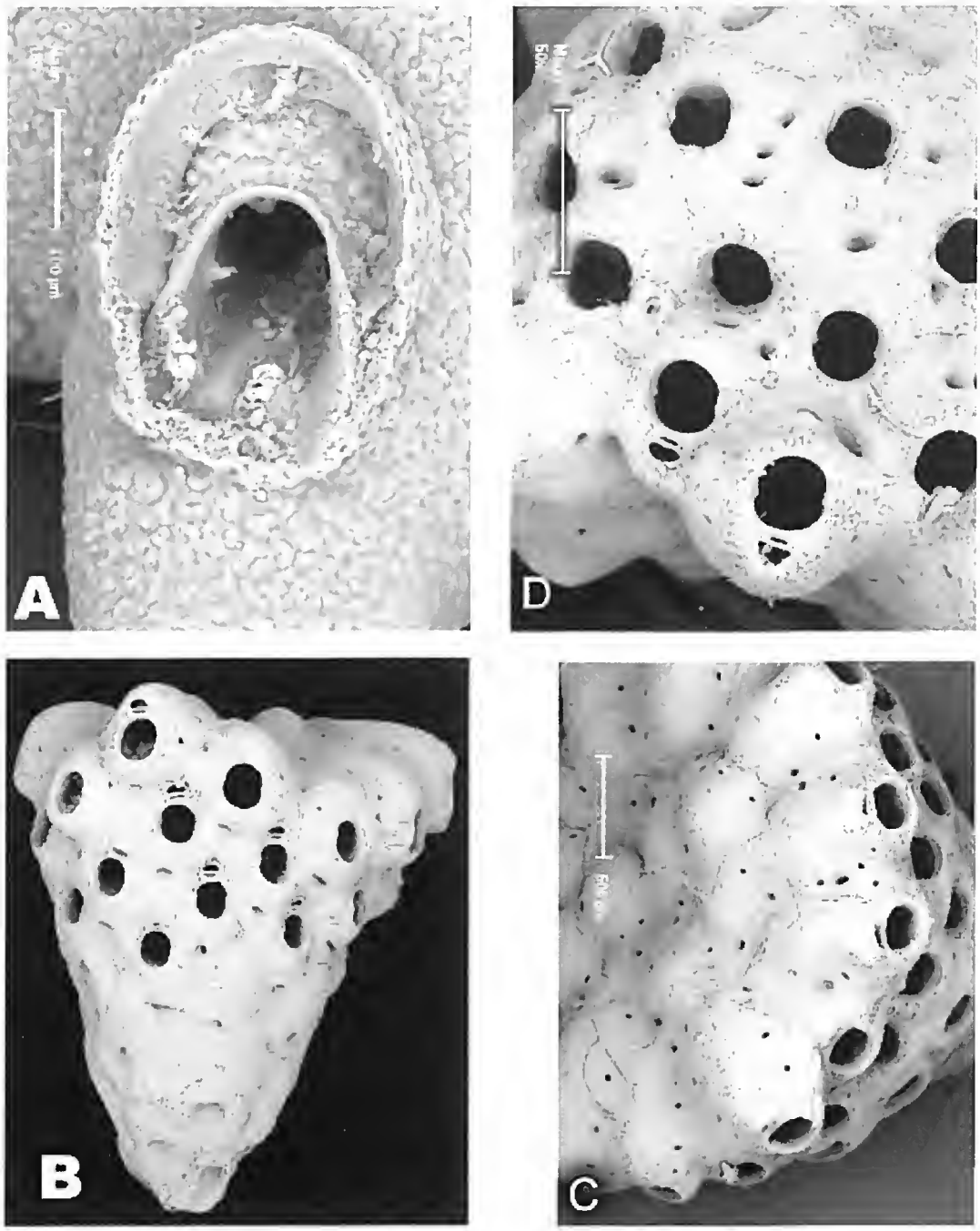


Fig. 2. A, *Batopora problematica* sp. nov. Paratype NMV F98032. Detail of broken ovicell showing relationship between peristome and ovicell, x170. B-D, *Lacrimula affinis* sp. nov. B. Holotype NMV F98033. Colony showing adapical kenozooids, x26. C. Paratype F98034, Antapical surface of colony showing frontal septular pores, x30. D. Paratype F98034, Orifices with avicularia, x47.

frontal budding, and a mode of life involving anehorage by rootlets into fine-grained substrata.

Measurements. Av. colony diameter 2.3 mm; height 1.1 mm; diameter of central kenozooid 0.30 mm; Lov 0.23 mm; lov 0.30 mm; Lor 0.11-0.12mm; lor 0.11-0.12 mm.

Lacrimula Cook 1966

Lacrimula Cook 1966: 217.

Type species. Lacrimula burrowsi Cook 1966: 218, pl. 2, figs 2, 3, 4, text-fig. 4A.

Description. Colonies stellate, conical or bell-shaped. Zooids alternating in whorls; zooid orifices large, with small paired condyles. Avicularia interzooidal or oral, small, with condyles or a bar. Adapical kenozooidal rootlet complex often associated with avicularia. Ovicells large, hyperstomial, closed by the operculum.

Remarks. Like *Batopora*, *Lacrimula* has a long fossil record, extending from the Eocene of Europe and also occurs in the Miocene of Indonesia (Cook & Lagaaij 1976). Recent species from the Indian Ocean tend to be from slightly shallower depths than those of *Batopora*, but the large numbers of colonies from over 1000 m off Australia suggest that species of both genera probably share a similar range.

Lacrimula affinis sp. nov.
(Fig 2B-D)

Holotype. NMV F98033, figured specimen SLOPE Stn 7.

Paratype. NMV F98034, figured specimen SLOPE Stn 7.

Other material. SLOPE Stn 7, 50 colonies, 8 with rootlets SLOPE Stn 6, 7 colonies, 1 with rootlet.

Etymology. affinis (L) - like, referring to the similarities with *L. burrowsi*.

Description. Large, conical *Lacrimula* colonies, with a heavily calcified adapical area formed by kenozooids. Zooids in whorls of 5-6, bulbous; primary orifices large, rounded, with small paired condyles; peristome absent. Zooid calcification coarsely granular, mainly imperforate except for few marginal septular pores. Avicularia small, rare, on the antapical side of the orifice, with a rounded rostrum and mandible slung on complete bar. Ovicells not found.

Remarks. L. affinis is very similar in appearance to *L. burrowsi* from the western Indian Ocean (Cook 1966). The colonies are of a comparable size, but the orifices of *L. affinis* are significantly larger than those of *L. burrowsi*. Colonies differ principally in the form and distribution of the avicularia and the small size of the orifice articular condyles. *L. burrowsi* frequently has large avicularia near the adapical region, but all the colonies of *L. affinis* have a massive development of secondary calcification in this region, and avicularia cannot be seen. The avicularia of *L. burrowsi* are interzooidal and have mandibles slung on elongated paired condyles; those of *L. affinis* are oral and antapical, and have a delicate complete bar. Ovicells in *L. burrowsi* and *L. pyriformis* Cook are known to be large, hyperstomial and closed by the operculum.

Measurements. Average colony diameter 2.5 mm; height 3.3 mm; Lor 0.23 mm; lor 0.22 mm; Lav and lav, 0.11 mm.

DISCUSSION

These records are the first for the family Batoporidae from the Australian region. The occurrence of *B. problematica* and *L. affinis* from deep water off eastern Australia extends the known distribution of both genera to the Tasman Sea, although species are known from Fiji and New Caledonia. An unnamed species of *Lacrimula* from deep water (677 m.) in the China Sea was illustrated by Cook (1981, Pl.C, fig. 3), but *Lacrimula sinensis* Lu (1991: 73, Pl. 20, fig.3), from the South China Sea, appears to belong to the genus *Characodoma*, as do also the specimens of *Osthimosia* species he figured. Colonies of *Characodoma* are frequently small, rooted, and associated with conescharellinid and batoporid species under "sand-fauna" conditions (Cadée 1987, Cook & Boek 1996, and Rosso 1999). The large number of colonies of Batoporidae in the Australian samples described here is the direct result of the method of collection by epibenthic sled. Both *B. problematica* and *L. affinis* were found from greater depths than other species, although the range of *B. murrayi* overlaps that of *B.*

problematica.

ACKNOWLEDGEMENTS

The specimens were collected on a voyage of C.S.I.R.O. MV "Franklin". Staff of the Museum of Victoria who participated in the sampling and sorting of this material include Dr Jan Just.

REFERENCES.

CADÉE, G. C., 1987. The shallow soft-bottom faunas of the Java Sea and Banda Sea. In *Bryozoa: Present and Past*, J. R. P. Ross, ed., Western Washington University, Bellingham: 49-56.

CANU, F. & BASSLER, R. S., 1923. North American later Tertiary and Quaternary Bryozoa. *United States National Museum Bulletin* 125: 1-302, pl.1-47.

COOK, P. L., 1966. Some "sand fauna" Polyzoa (Bryozoa) from Eastern Africa and the northern Indian Ocean. *Cahiers de Biologie Marine* 7: 207-223.

COOK, P. L., 1981. The potential of minute bryozoan colonies in the analysis of deep sea sediments. *Cahiers de Biologie Marine* 22: 89-106.

COOK, P. L. & BOCK, P. E., 1996. *Characodoma* Maplestone, a senior synonym of *Cleidochasma* Harmer (Cleidochasmatidae). In *Bryozoans in Space and Time*, D. P. Gordon, A. M. Smith & J. A. Grant-Maekie, ed., NIWA, Wellington: 81-88.

COOK, P. L. & LAGAAIJ, R., 1976. Some Tertiary and Recent coneseharelliniform Bryozoa. *Bulletin of the British Museum (Natural History), Zoology* 29: 317-376, pl. 1-8.

GORDON, D. P., 1985. Additional species and records of Gymnolaemate Bryozoa from the Kermadec region. *Records of the New Zealand Oceanographic Institute* 4: 160-183.

GORDON, D. P., 1989. The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomida Aseophorina) from the western south Island continental shelf and slope. *New Zealand Oceanographic Institute Memoir* 97: 1-158, pl. 1-50.

GORDON, D. P. & D'HONDT, J.-L., 1997. Bryozoa: Lepraliomorpha and other Aseophorina from New Caledonian waters. *Mémoires du Muséum National d'Histoire Naturelle* 176: 9-124.

HAYWARD, P. J. & COOK, P. L., 1979. The South African Museum's Meiring Naude Cruises. Part 9, Bryozoa. *Annals of the South African Museum* 79: 43-130.

D'HONDT, J.-L., 1986. Bryozoaires de Nouvelle-Caledonie et du plateau des Chesterfield. *Bulletin du Muséum national d'histoire naturelle* série 4, 8A (4): 697-756.

LU LINHUANG, 1991. Holoeene bryozoans from the Nansha sea area. In *Quaternary Biological Groups of the Nansha Islands and the Neighbouring Waters*, Edited by the Multidiseiplinary Oceanographic Expedition Team of Academia Sinica to the Nansha Islands, Zhongshan University Publishing House, Guangzhou: 11-81, 473-486, pl. (Section 2) 1-21.

NEVIANI, A., 1901. Briozoi neogenici delle Calabrie. *Palaeontographia Italica* 6 (1900): 115-266.

PIZZAFERRI, C. & BRAGA, G., 2000. Nuove osservazioni sullo sviluppo astogenetico di *Batopora rosula* (Reuss), Bryozoa Cheilostomatida del Miocene del Pedeappennino Parmense. *Annali dei Museo civico - Rovereto* 14 (1998): 55-88.

REUSS, A. E., 1867. Über einige Bryozoen aus dem deutsehen Unteroligozän. *Sitzungsberichte der Akademie der Wissenschaften in Wien (Abt. I)* 55: 216-234.

REUSS, A. E., 1869. Paläontologische Studien uber die älteren Tertiärschiehten der Alpen, II, Die fossilen Anthozoen und Bryozoen der Schichtengruppe von Crosara. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien* 29: 215-298.

ROSSO, A., 1999. Reeent and fossil speeies of *Characodoma* Maplestone from the Mediterranean with deseription of two new speeies. *Journal of natural history* 33: 415-437.

Manuscript received 22 December 2003
Revision accepted 21 July 2004

TRANSACTIONS

OF THE

ROYAL SOCIETY OF VICTORIA

SOME REMARKS ON THE 1998 SYDNEY-HOBART RACE

P.N. JOUBERT OAM

INTRODUCTION

The 1998 Sydney-Hobart race was sailed in the worst weather on record, a number of yachts were overturned, some were lost, six people lost their lives and there were some amazing heroic efforts by rescuing helicopter crews.

These remarks are mainly about the winds and waves, which were unique.

The race is sailed from Sydney on the east Australia coast, southwards to a turning point off the island on the south-east corner of Tasmania and thence to the port of Hobart (fig1). It is a great race with a great tradition standing equal with both the Fastnet race, run by the Royal Ocean Racing Club of England, and the Newport-to-Bermuda race run by the Cruising Club of America.

Because of natural circulations in the large oceans, there is a southbound current flowing down the eastern Australian coast. Its penetration southwards varies, as does its speed of flow. On the occasion of the 1998 race it was flowing as strongly as I had ever seen it. It was flowing at 4 to 5 knots in a broad stream almost into the coast and it was still flowing strongly south of Gabo Island, which is the last point on the east coast before the yachts cross Bass Strait. It is most likely it had an effect on the steepness of the waves generated by the low pressure system.

That the current was so fast is confirmed by the presence of almost the entire fleet to the east of Gabo Island as reported at the 2.00 pm radio schedule 7th December which is 25 hours after the start and a distance of 230 nautical miles from Sydney.

Bass Strait is about 200 nautical miles wide at its eastern end but narrows to about 120 miles near its centre. It is shallow, under 100 fathoms down to 30 fathoms over much of the region, and notorious for the generation of low barometric pressure systems and accompanying steep waves with the strong winds. It is also a tidal basin with significant tidal flows.

The race started on Boxing Day, 26th December, in a fresh north-easterly breeze and the fleet sailed south with spinnakers flying. At the 2.00 pm radio schedule on 27th December, the weather report was read and a 45 to 55 knot storm warning was issued. During the schedule, when every yacht is contacted and reports its latitude and longitude, any further communication is discouraged. One yacht, Sword of Orion, broke the pattern of response and reported that they were experiencing winds of over 70 knots.

Larger yachts ahead of Sword of Orion had also experienced these hurricane force winds earlier but had not reported them under the rules of yacht racing concerned with outside information.

THE WEATHER

The Australian Bureau of Meteorology were the advisers to the race organizers and the competitors. At a briefing on the 24th December they were unsure how the weather pattern might develop but indicated that weather conditions might become hazardous.

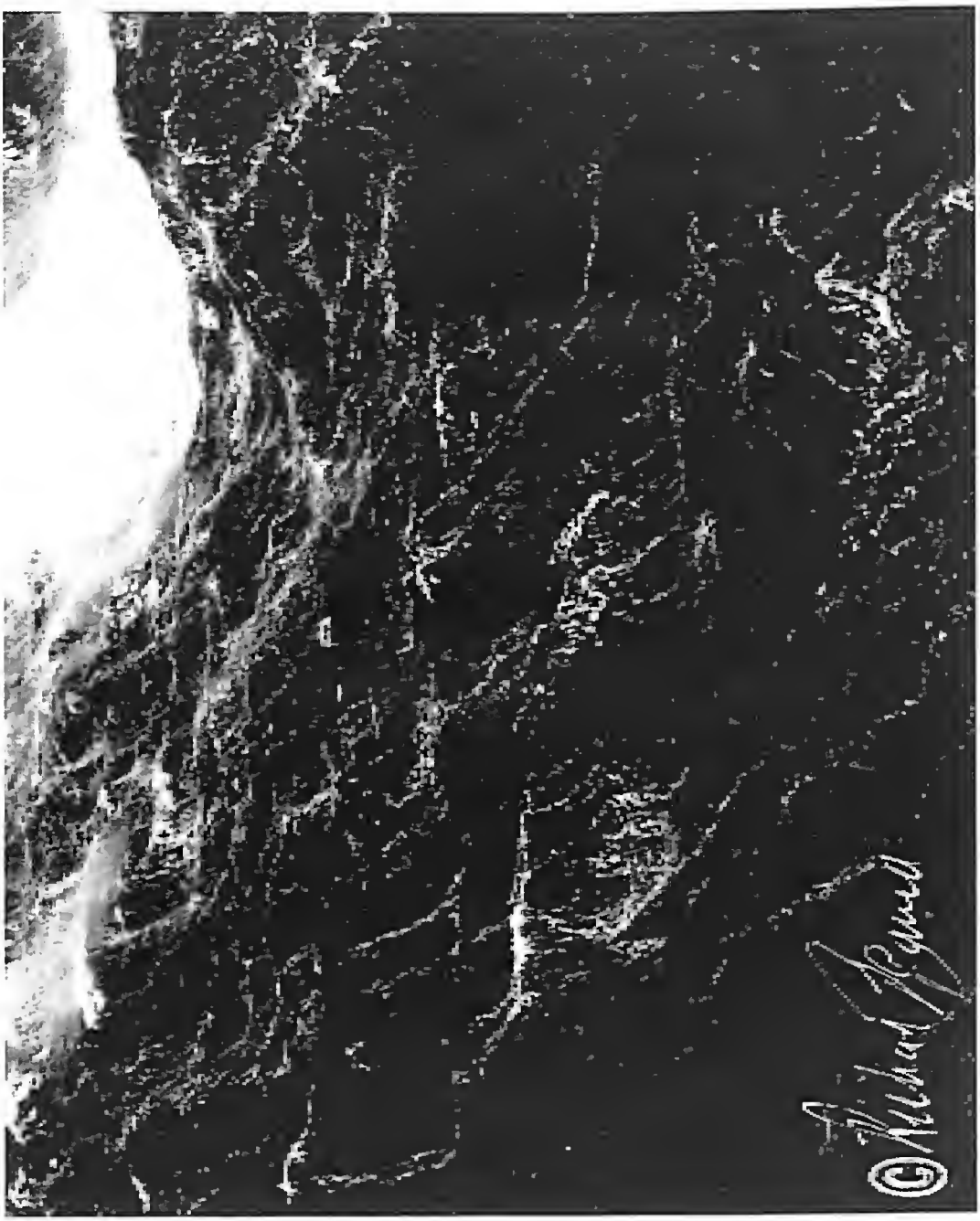
A gale warning was issued before the start of the race on December 26th at 9.00 am.

One hour after the race had started this was upgraded to a storm warning with winds of 45 to 55 knots predicted for the afternoon of the 27th December in Bass Strait.

Since the event, the Bureau has strongly contended that within this forecast of mean speeds is an expectation of gusts to 70 knots. (ref. 1). However, there were not many competitors who appreciated this point as, to my knowledge, it had not been mentioned at the oral briefings.

A gust is defined as lasting less than 10 minutes.

Peter Joubert has competed in 27 Sydney-Hobart races, being skipper on 24 occasions. He designed all the yachts in which he has competed. Kingurra designed in 1972, is a timber yacht 43 feet LOA, of 13 Tons displacement and has competed in 13 Sydney-Hobart races. The yacht was dumped almost upside down by a giant wave at about 7.00 pm on 27th December but returned upright within about ten seconds. One crew member was lost overboard, to be safely rescued sometime later by a Victorian Police helicopter.



Of course, to obtain a mean of 50 knots with gusts to 70 knots there would have to be an equal time with gusts of only 30 knots, or its equivalent. This was not observed on Kingurra. What was observed on Kingurra from 3.00 pm to the time when the yachts was dumped by a giant wave at about 7.00 pm, were wind speeds greater than 60 knots. There were only a few short periods when the speed gave a reading below the instrument maximum of 68 knots. Judging by the note of the wind, there were many periods when it was much greater than 68 knots, but how great I cannot say.

In the report of the review committee of the Cruising Yacht Club of Australia (ref. 2) into the 1998 Sydney-Hobart race, on page 45, lines 1-4, it is stated, "most yachts will have recorded apparent wind speeds on board up to about 8 knots faster than the true wind speed due to the effect of the speed of the yacht. Thus average observed wind speeds would have been 60-62 knots with gusts in the low 70 knot range."

What has been neglected in this correction to the wind speed is the effect of heeling of the yacht on a masthead mounted cup anemometer. The speed registered will decrease from the true speed as the cosine of the angle of the heel to the true wind direction. So for a 30° angle of heel, measured in the plane of the true wind, the anemometer would under-read by 13%. Thus the average observed wind speed for a heeled yacht sailing across the wind at 8 knots would have been 69 to 71½ knots with gusts over 80 knots. If the boat speed is less than 8 knots, then the true wind speed is greater. (see fig 2)

If the yacht's path is angled at other than 90° to the true wind speed then the additive effect of heeling is less and so on through all the complications of relative motions.

Suffice to say that the correction suggested in the CYCA report is simplistic and neglects other more important corrections of the opposite sign.

The light house at Wilson's Promontory reported a wind reading at 6.00 am on 27th December of 71 knots and at 9.00 am of 79 knots. These readings are ten minute averages and the maximum gust recorded was 92 knots. Higher wind recordings from Wilson's Promontory relative to those at other near locations are often observed due to the local topography. In this instance the readings at Wilson's Promontory were not reported to the yachting fleet. The Coroner remarked (p. 104) that, "this was the highest recording of wind speed at Wilson's Promontory for the month of December since accurate wind recordings were commenced in 1998" and on p.127 he found, "that the wind strength at Wilson's Promontory should have been conveyed to the Race Fleet as soon as it was known".

Better evidence on wind speeds is forthcoming from the pilot of the Victorian Police Rescue helicopter which was involved in the rescue of the crew man lost overboard from Kingurra. The pilot of the helicopter, Senior Constable Darryl Jones, presented sworn evidence to the Coronial inquiry on the deaths in the 1998 Sydney-Hobart race (ref. 3). He states that between 4.00 pm and 6.00 pm on 27th December, while flying to the east over the Victorian mainland, he encountered tail winds of 85 knots.

After refuelling at Mallacoota he was directed by ground control to the yacht Kingurra who had reported a man overboard. Kingurra at 2pm was in a position 38°07'S 150°46'E about 45 nm SE of Gabo Island, which is the most southerly point on the east coast and therefore receiving the full force of the winds and the waves moving through Bass Strait.

He states "we arrived overhead this position in approximately 15-20 minutes where the conditions could only be described as incredible. I have never seen the sea in such a wild and horrendous state. There were rain showers and continuous sea spray and the cloud base ranged from 600 to 2000 feet. We were faced with waves and swells between 80-90 feet in height (see figs 3 and 4) and the occasional wave up to 120 feet. The winds were ranging between 70 to 80 knots...."

So the more precise reading of Senior Constable Jones in his helicopter as he hovered is in good agreement with the value found from the CYC report on wind speeds when corrected for angle of heel as done previously, namely 68-70 knots.

This suggests that the forecast value of 45-55 knots from the Weather Bureau is less likely to be a proper measure of the wind speed.

It should be noted that the force of the wind on masts, hulls, sails, crew members and waves is proportional to the square of the velocity. Hence the wind force predicted from the Weather Bureau is half that due to a wind of 70 knots.

It should also be noted that the reading of wind speed by the helicopter was observed when it was at low altitudes so any possible effect of wind variation with height above the seas would not apply.

WAVE HEIGHTS

There is a significant difference between the wave heights as predicted and as measured by the helicopter.

Normal wave theory predicts wave heights which depend on variables such as fetch, wind speed and the time the wind has been blowing. An extract from the Guide to Wave Analysis and Forecasting (ref. 4) is shown as figure 5 where the above three independent quantities are the variables in the predicted heights of the waves.

Due to inequalities, not all waves generated are of the same size nor travelling at the same speed or direction and thus can produce a rearrangement with all the

energy going into one wave which is larger and will reach the Stokes peak and break. Currents flowing against the direction of the waves can increase their size significantly. As well there may be swells approaching from a variety of directions as a result of distant storms. Passing crests are additive and add to the extremes.

Predicted wave heights of 4 to 7 metres were generally forecast in the Bureau's storm warning while infrequent maximum waves with heights to 13 metres could be expected. Of course, this is a prediction based on the mean winds in the storm being only 45-55 knots. If the mean wind speed was greater then obviously this standard theory will prediet greater

wave heights.

The Polair helicopter flown by Senior Constable Jones carried a radio altimeter whose function is to measure the height of the helicopter above the ground (or sea) in close proximity. I have to hand a copy of the specification which includes a claimed accuracy of ± 2 feet for heights greater than 40 feet. It would be one of the most accurate devices available for measuring wave heights.

Senior Constable Jones had 12 years experience in the Victorian Police air wing and has flown on a number of hazardous missions. He is a highly trained and skilled pilot and there is absolutely no reason to doubt his observations.

In his sworn statement to the Coronial Inquiry, at the point in his evidence where they had located the lost overboard crewman from Kingurra, John Campbell and the rescuing policeman, Senior Constable Key, was in the water near Campbell, Senior Constable Jones continues, "Key was winched into the water whilst I held a 100 foot hover above the man. Hovering was extremely difficult as I had no reference by which to hold the helicopter in position and Senior Constable Barclay (the crewman observer and winch controller) was constantly talking me into position. Senior Constable Barclay advised me that he would have to pay out a large amount of winch cable due to the size of the swell. Whilst hovering I observed a wall of water coming towards us and confirmed with him that there was plenty of cable out because I had to make an urgent climb to avoid being hit by this wave. He advised me to 'go ahead' and I climbed another 50 feet. This wave passed under the helicopter by approximately 10 feet. I am able to state this because the helicopter is fitted with a radio altimeter which displays the height of the ground or water and I noticed that it reduced to 10 feet as I climbed".

Thus the height of this particular wave was 140 feet which is the largest ever recorded.

One of the highest waves to be measured previously, occurred in Hurricane 'Luis' and was reported by the Master, Captain R.W. Warwick and nine of the officers of the watch of Queen Elizabeth II. The height of the wave was 29 metres and was confirmed later by a nearhy Canadian weather buoy which recorded one wave at 30 metres. The report of the event was published by the Meteorological Office in 1996 (ref. 5).

An even larger wave of 34.1 metres was measured by a qualified observer aboard the USS Ramapo in a typhoon in 1933. The measurement was by triangulation and doubters have re-examined the mathematics of that incident ever since.

A letter published in the Seahorse Magazine, October 1999, about aspects of the Sydney-Hobart race by Mr. Kalaugher (ref. 6), suggested that "one wave from a photo had been estimated to be 110 feet high." This produced a comment from an experienced person, Mr. John De Bruin, who stated in his response published in Seahorse Magazine, July 2000, page 28 (ref. 7), as follows: "One remark of Mr. Kalaugher's that I do want to question, however, is that 110 foot wave. I have quite a reasonable amount of offshore experience gained in both the Atlantic and Southern Oceans. Wave height is exponential to strike length and the strength of counter currents. The 1998 Hobart depression encountered a south-going current. Yet the time (of building up) and speed of this depression make it hard to believe 110 foot waves could have developed".

Mr. De Bruin continues with his comments and states "in the Southern Ocean, waves of over 60 feet are considered exceptional, even over the flats to the South of Cape Horn.

In the North Atlantic (my playground) waves of 60 feet or more are rare and are most usually linked to former tropical storms..."

So here lies the heart of the dichotomy of opinion. On the one hand, we have a measurement by a calibrated instrument in the centre of the storm and on the other, disbelief by sailors where the measurement disagrees with accepted theories and their own experience.

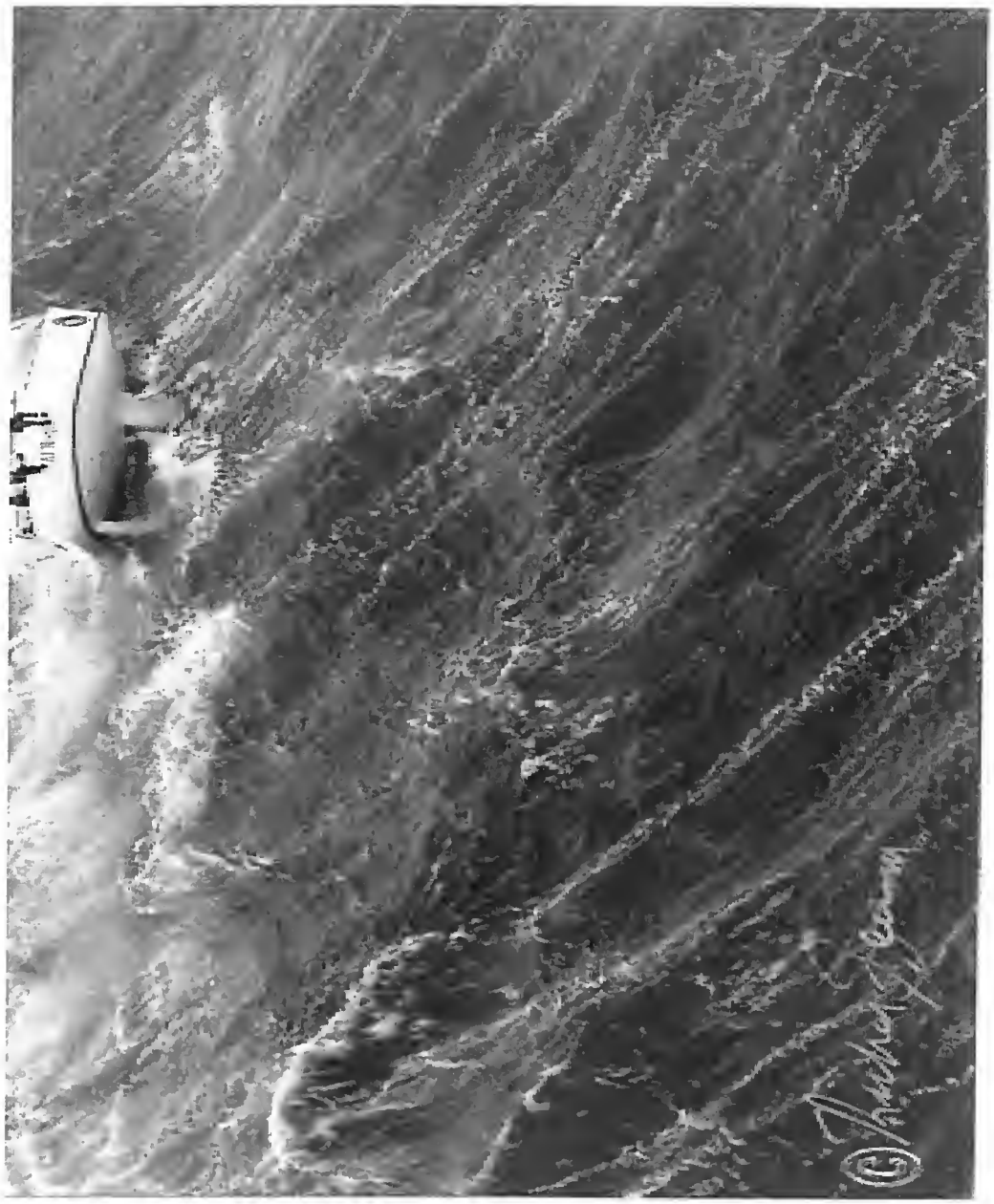
Support for the measurement comes from the work of Dysthe and Harbitz (ref. 8) who introduced a simple theoretical model to analyse how a polar low can produce a severe sea condition. When the centre of the low moves with a velocity V having a relationship to the component of wind velocity in the direction of motion U, then a phenomenon known as group velocity quasi-resonance exists. There is then a spectral component in the wave field near the velocity of the storm which will stay in the enhanced wind field of the storm for some time. The phenomenon is also known as fetch enhancement.

In particular :

I. when $V/U<0.25$, the storm motion is too slow to give quasi resonance (fetch enhancement) for the wind field under examination.

II. when $0.25<V/U<0.5$, extended development of waves is possible.

III. when $V/U>0.5$, the polar low will mostly outrun the spectral development at an early stage.



Mr. Jeff Callaghan of the Bureau of Meteorology presented a paper on the development of freak waves near intense lows and tropical cyclones at a conference in December 1999 (ref. 9). I am indebted to him for drawing my attention to the phenomenon of quasi resonance and for allowing me to reproduce part of his paper.

The low in Bass Strait was moving at about 20 knots and its track is shown in figure 4. So conditions were in agreement for quasi-resonance with wind velocities of 70 to 80 knots giving V/U = 20/75 = 0.27. The portion of the yacht fleet that experienced the cyclonic winds of 70 to 80 knots from 1400 EDST on December 27th, were in the precise position to be

beset by waves that had suffered fetch enhancement over a shallow sea for over nine hours beyond Wilson's Promontory.

The paper by Greenslade describing a subsequent wave modelling study of the events (ref. 10) draws attention to the large 11 second period swell running to the south west as a result of a low pressure system in the Tasman Sea. He remarks (p.56) that this storm had a significant effect on the sea state near the coast. He further suggests that the change in direction of the east Australian current to the east near Gabo Island would increase the size of these waves as well as shortening their period.

WEATHER PREDICTION

The associated major contradiction involves the weather report and the actual measurements of wind velocity. How is it that the wind velocity measured close to the top of the waves by the hovering helicopter was 70 to 80 knots and the weather forecast prediction was 45-55 knots?

The answer may well be given by the manner in which the weather is predicted and the relatively small size of the storm.

Weather is predicted by two methods, one by the meteorologist and the other by the computer. The data needed includes surface and upper air measurements of pressure, temperature, moisture and wind.

A paper describing these techniques and procedures was presented at a Workshop on Safety of Ocean Racing Yachts by Mr. Patrick Sullivan (1999). (ref. 11)

The data is arranged on a grid on numerous levels from the surface to the stratosphere which may look like his figure 1, reproduced here as figure 4. The computer then processes the data to produce the forecast. There are many prediction models and they continue to be improved. A number of these models were used on Saturday 26th December and none predicted the highest winds.

Mr. Sullivan points out that patterns at the surface can be drastically changed in 6-12 hours by complex interactions high in the atmosphere. The intense low started to develop over western Bass Strait early on the 27th and had intensified to hurricane strength by 3.00 pm. It is considered by some that with a global grid, the grid points are too far apart (about one degree) to properly predict a local event.

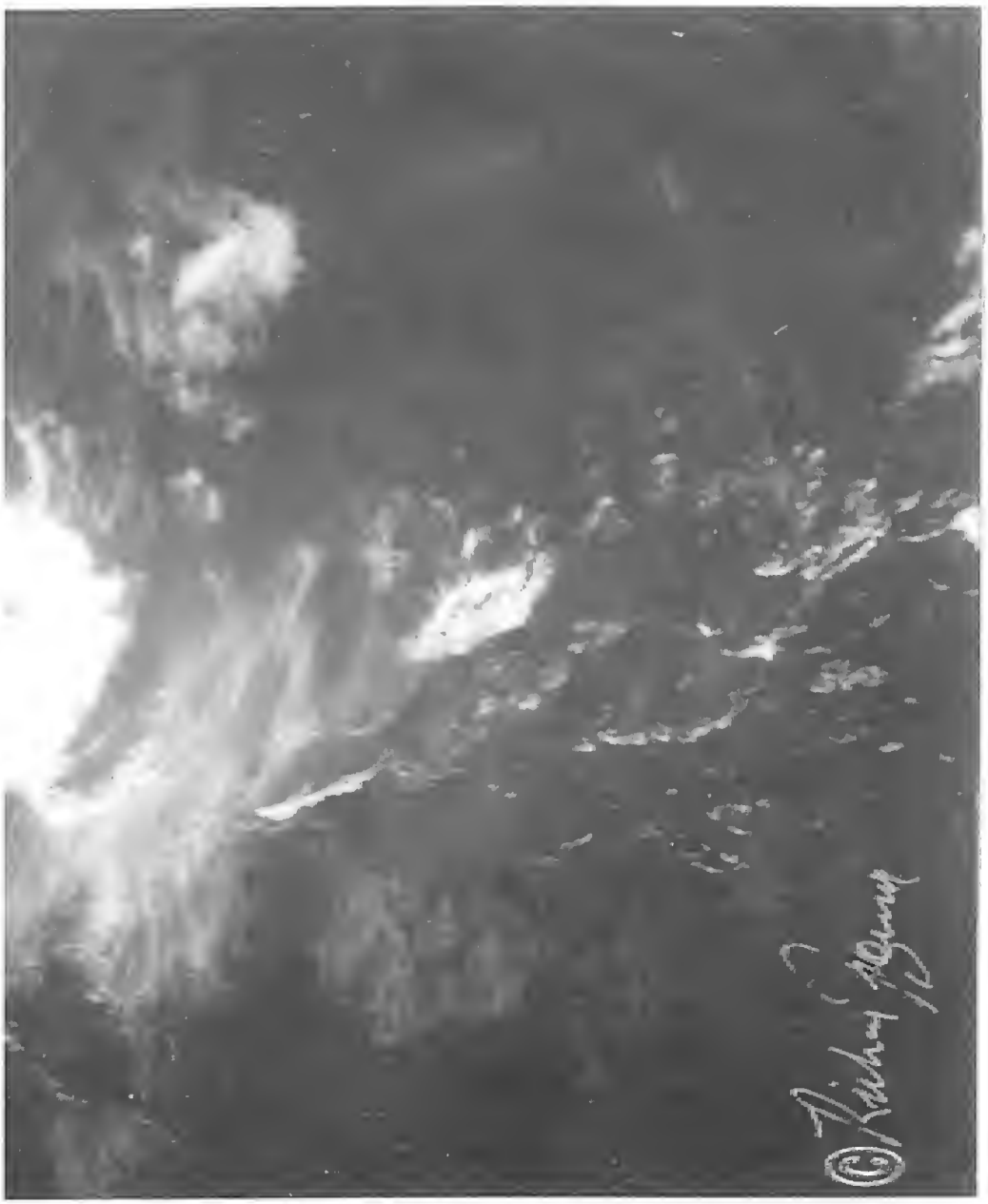
Finer spaced regional models can be used which cover only a portion of the globe. A 25 kilometre resolution model was the basis of the 2.00 pm forecast by the Bureau of Meteorology on the Saturday 26th which predicted the 45-55 knot winds.

Even with this localized smaller grid, the computer model was too bland in its prediction.

Intense localized high latitude vortices that often resemble hurricanes have been observed in the northern hemisphere and the Sydney-Hobart storm may well have been one such. Emanuel and Rotunno (ref. 12) remark that polar lows appear to form in polar air with strong zonal flow aloft.

O.M. Phillips in a private communication remarked, "From what little information I had before, or have gleaned from what you sent, it seems that this violent occurrence was probably one of the very intense polar storms that have been identified in the last few years since the advent of polar imaging satellites. I have seen images of several arctic storms in the region north and west of Norway: They are characterized by a tight structure, true hurricane force winds but relatively small scale compared with low-latitude hurricanes. (In this sort of storm, the size is inversely proportional to the Coriolis parameter, the vertical component of the earth's rotation, which is of course largest near the poles). This is the first time I have seen what could be a southern hemisphere analogue. Because of the relatively small scale of the phenomenon, it is maybe not surprising that wind speeds measured some distance (50 or so km) away from the location of wind maximum, should be substantially less. It was clearly a very violent affair, and I am not sure present-day ocean wave generation models could provide good information on the waves, even if the wind information grid were dense enough to resolve the structure of the event."

Graham Mills of the Bureau of Meteorology Research Centre has subsequently reanalysed the data using five varying size grids (0.75° down to 0.05°) which has shown the development of the hurricane much more closely. (ref. 13 and 14). This not only shows the intensity but also the localized concentration of the very strong winds. The more closely spaced grids forecast stronger winds greater than 30 m/s. The interaction of the variables are fully discussed in these two recent papers. Both authors, Mills and Greenslade, compared their revised analyses of winds and waves, respectively, with readings from stations that were located some significant distance from the location of the helicopter at the time of the rescue of the man lost overboard from Kingurra.



CONCLUSIONS

There is strong evidence which suggests one of the waves generated in Bass Strait on 27th December 1999 was the largest ever measured at 140 feet.

The winds were of hurricane strength and were greater than 70 knots in speed.

The storm was localized and may have been a southern counterpart of an Arctic low.

Conditions appear to have favoured "quasi resonance" as the cause of the extreme waves. As well, a strong counter current of 4 to 5 knots associated with a swell from the north east of about 11 seconds period had a contributing effect.

Computer made the ??? of the weather with even

more precise models applied after the event , were unable to predict the localised extreme events.

REFERENCES

(1) *Preliminary report on meteorological aspects of the 1998 Sydney to Hobart yacht race.* Bureau of Meteorology, February 1999.

(2) *Report of the 1998 Sydney Hobart race review committee.* Cruising Yacht Club of Australia, May 1999.

(3) *Coronial inquiry into deaths in the 1998 Sydney-Hobart race.* Statement by Senior Constable Darryl

Jones 21590, Line Pilot, Police Air Wing.
(4) *Guide to Wave Analysis and Forecasting* WMO – No. 702 (1998).
(5) The Meteorological Office 1996: Hurricane Luis, The Queen Elizabeth and a rogue wave, *The Marine Observer*, 66: 134-137.
(6) *Seahorse*, October 1999. Letters, p.32 by Mike Kalaugher.
(7) *Seahorse*, July 2000. Letters, p.28 by John de Bruin.
(8) Big waves from polar lows. Dysthe, K.B. and Harbitz, A. *Tellus* 39A, 500-508, 1987.
(9) Development of freak waves near small intense lows and tropical cyclones. Callaghan, J. *7th National Australian Meteorological and Oceanography Society Conference Melbourne*, December, 1999.
(10) A wave modelling study of the 1998 Sydney to Hobart yacht race. Greenslade, D.J.M., *Aust. Met. Mag.*, 50, 53-63, 2001.
(11) Can we predict the weather? Sullivan, P *Proceedings workshop on safety of ocean racing yachts*, University of New South Wales, Sydney Australia, 5-12 March, 1999.
(12) Polar lows as artic hurricanes. Emanuel, K.A and Rotunno, R., *Tellus*, 1-17, 41A, 1989.

THE SNOWY RIVER DEBATE

Brian L. Finlayson

School of Anthropology, Geography and Environmental Studies, The University of

Melbourne, Victoria 3010, Australia

The present debate about the use of the Snowy River's water is only about a decade old, despite the fact that the scheme to divert water was completed nearly 40 years ago. In this paper the origins and trajectory of the current debate are reviewed, particularly in relation to the physical nature and condition of the river itself. The nature of the river will be discussed in relation to its four major sections each of which has specific physical characteristics and has been affected differently by the building of the Snowy Scheme.

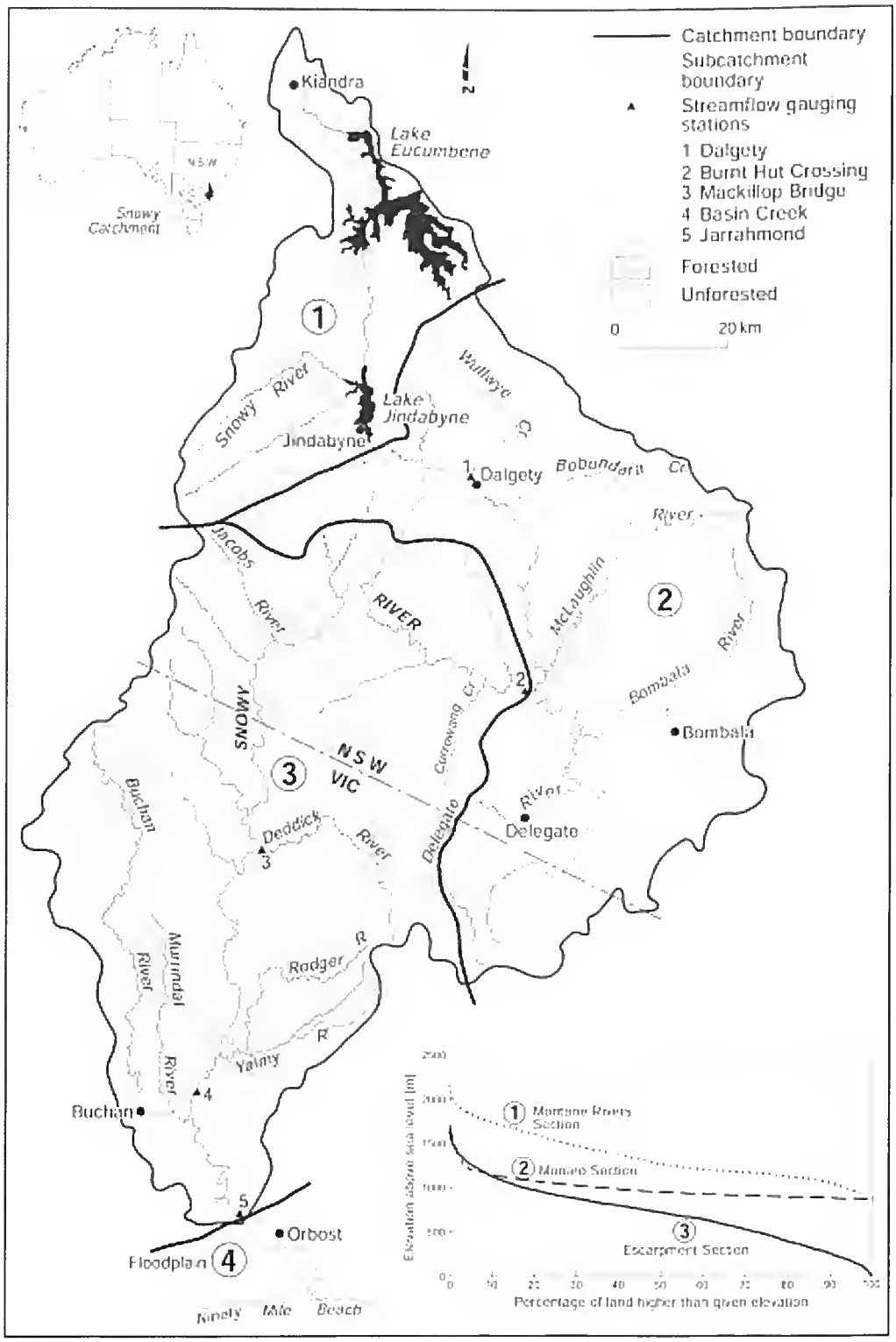
Not all of the problems of the Snowy River are the result of flow diversions through the Snowy Mountains Scheme; there is a long history of human intervention through desnagging, clearing riparian vegetation, levee building, draining floodplain wetlands, etc. The problems on the Snowy are shared by many other rivers in Victoria, most of which are in worse environmental condition. In the Snowy River debate, the iconic status of the Snowy and its location in a politically sensitive electorate has given it a head start over other perhaps more deserving cases in the battle for river management resources.

THE diversion of flow from the Snowy River into the westward-flowing systems of the Murray and the Murrumbidgee Rivers has recently been the subject of a vigorous public campaign, both in New South Wales and Victoria. There has been a tendency in that debate to treat the Snowy River as a single river with a single issue – the diversion of flow – yet the character of the river varies significantly along its 489 km course, as does its management history and its responses to flow diversion. In addition to this long history of human intervention in the river system, the Snowy debate is complicated by the fact that it lies within two jurisdictions, New South Wales and Victoria, and the Commonwealth Government is also involved, initially through the defence powers of the constitution and more recently as a driver of micro-economic reform through the Council of Australian Governments (COAG).

We have reached a point in the development of Australia's water resources where it is no longer possible to continue with what Graeme Byrne (2000) calls the "Fordist" model of river utilization where rivers are viewed as conveyor belts devoted to energy, transport and chemically intensive agriculture which has led inevitably to environmental degradation and the loss of valuable environmental services. The attainment of the present level of environmental degradation is concurrent with the rise of ecological politics. This is not a simple matter of cause and effect. Past examples of severe degradation of river systems, such as the pollution of rivers in mid-nineteenth century Britain, or the despoiling of Victoria's rivers at about the same time by mining waste, produced corrective actions from governments but did not spawn an ecologically based political movement.

Another driver of the environmental rehabilitation of the Snowy River has been government microeconomic reform. Accordingly, the Snowy Mountains Authority has been corporatised, with the shareholders of the corporation being the NSW, Victorian and Federal Governments. To provide some level of operational certainty to the new corporation (Snowy Hydro Limited) the controlling governments have sought to deal with the environmental issues on the Snowy prior to corporatisation. Thus the licence under which Snowy Hydro operates specifies how, and how much, water will be returned to the environment and who will pay the associated costs (Vanderzee & Turner 2002).

A central principle of the microeconomic reform process is to put market forces between the government and the electorate in order to move governments away from the temptation to indulge in 'pork-barrelling' (G. Byrne, pers. comm. 2003). As will become obvious later in this discussion, in the case of the lower Snowy River in Victoria, this has been spectacularly


Catchment boundary
Subcatchment boundary
Streamflow gauging stations
1 Dalgety
2 Burnt Hut Crossing
3 Mackillop Bridge
4 Basin Creek
5 Jarrahmond
Forested
Unforested
0 20 km
Snowy Catchment
NSW
Kiandra
Lake Eucumbene
Snowy River
Lake Jindabyne
Jindabyne
Wullwye Ck
Dalgety
Bobundara Ck
River
Jacobs River
RIVER
McLaughlin River
Bombala River
Bombala
Corrowong Ck
SNOWY
NSW
VIC
Delegate River
Delegate
Buchan River
Deddick River
Murrindal River
Rodger R
Yalmy R
Buchan
Orbost
Floodplain
Ninety Mile Beach
Elevation above sea level (m)
1 Montane Rivers Section
2 Monaro Section
3 Escarpment Section
Percentage of land higher than given elevation

unsuccessful, as political, rather than scientific, considerations have driven the allocation of resources for river restoration.

THE SNOWY BASIN LANDSCAPES

The Snowy River has its source in the Australian Alps, on the eastern side of Mt Kosciusko and flows in a generally southerly direction to the sea on the Ninety Mile Beach on the Bass Strait coast of Victoria (Fig. 1). The basin can conveniently be subdivided into four sections as shown in Figure 1, primarily on the basis of topography. These are shown in Figure 1 and topography is described by the hypsometric curves, a cumulative plot of area against elevation above sea level that provides a 'shorthand' description of relief. These sections generally correspond to the geomorphic regions of Jennings and Mabbutt (1985), namely the Australian Alps (Section 1), the Monaro Tableland (Section 2), the East Victorian Uplands (Section 3) and the Gippsland Plain (Section 4). Section 1 is referred to in the Snowy Water Licence as "The Snowy Upper Montane Rivers" and consists of that part of the basin upstream of the Jindabyne Dam; Section 2, the Monaro, lies between the Jindabyne Dam and the junction of the Snowy River with the Delegate River; Section 3, the escarpment, is that section of the catchment where the river traverses the escarpment which separates the plateau of the Monaro from the coastal plain; and Section 4 is the floodplain of the lower Snowy River (Fig. 1).

The Montane Rivers

This section, because of its elevation, produces the highest runoff per unit area in the catchment. With only 14% of the total catchment area it generates nearly half of the mean annual flow. This is a plateau with little dissection by river valleys (Fig. 1) and while all the dams have been built here it is probably the case that there are much better dam sites further down the system, especially in Section 3. Of the four sections of the basin, this one has been most severely impacted by the construction of the Snowy Mountains Scheme, yet most published discussions of the effects of the Scheme on flow do not mention the rivers in this part of the basin. Land use in this section is predominantly public open space (shown shaded in Figure 1), notably Kosciusko National Park, and some private farmland.

The physical works of the Scheme are located only in this section of the basin. There are two large dams; Eucumbene and Jindabyne, both of which flooded extensive farmland and two towns, Adaminaby and Jindabyne; and two small pondages at Guthega and Island Bend. The social impact of the scheme here was significant with people being forced off their farms and forced out of their homes and businesses in the flooded towns. To the extent that there were environmental controls applied in the original Snowy Project, this is where they had effect though concern for the natural environment was clearly not high on the agenda of the project's builders. Collis (1990) reports the clashes that took place between Sir William Hudson, the engineer in charge of the construction program, and the administration of the Kosciusko National Park over his use of willows in river stabilisation works in the Park.

Collis also reports that strict environmental guidelines were built into the Snowy Mountains Hydro-Electric Power Act. This is, in a sense, true but with a very limited conception of what "environment" means. The matters covered in the Act dealt mainly with sediment yield and had a self-serving interest for the Snowy Mountains Hydro-Electric Authority (SMA). These controls had the purpose of minimising sediment yield into the Authority's reservoirs, thereby extending their effective storage life. Although Collis' book was published as recently as 1990, references to "environment" are mainly in relation to the Kosciusko National Park. While he says nothing about concerns over the environmental condition of the rivers whose flow had been regulated by the scheme, Collis nevertheless claims "The Scheme pioneered responsible environmental attitudes in engineering" (p280).

The impact of the Snowy Scheme on the montane rivers is difficult to elucidate. The original SMA published records of flow up to 1970 (Snowy Mountains Hydro-Electric Authority 1970,1971), which was only three years after the completion of the Jindabyne Dam. All data for this section of the catchment now resides with the newly corporatised Snowy Hydro and they are not available to anyone outside the corporation on the grounds that they are commercial-in-confidence (M. Clayton pers. comm. 2003). Using the data published in 1970 it is possible to get some indication of the nature of the flow modifications the montane streams have experienced.

Fig. 1. The Snowy River catchment showing the four sections discussed in this paper with hypsometric curves for sections 1, 2, & 3. (Hypsometric curves produced by Dr David Wilson, Department of Civil and Environmental Engineering, The University of Melbourne).

Figure 2 shows the mean monthly flows for the Eucumbene River at Eastbourne, a gauging station on the Eucumbene River between the Eucumbene Dam and Jindabyne, for the pre-regulation and post-regulation periods. Little, if any, flow is released from Eucumbene and the recorded flows at Eastbourne post-regulation are mainly derived from unregulated tributaries downstream of the dam.

The licence under which Snowy Hydro operates provides for environmental flows in these rivers but although the total quantity of water is specified – sufficient to generate 100 GWh, rising to 150 GWh in 8 to 10 years – as at the end of 2003, no flow requirements had been devised and there had been no action to implement this provision. The licence requires the environmental flows to mimic natural flows under prevailing climatic conditions to the extent possible. Since all the data are kept by Snowy Hydro and are commercial-in-confidence, how will compliance with this vaguely worded condition be monitored? There is no possibility of independent audit and no transparency.

The Monaro

This section of the Snowy is the real focus of the movement, which developed during the 1990s, pressing for return of flows to the Snowy. Like the montane rivers section, the Monaro is a plateau, little dissected by the rivers that cross it (Fig. 1). The majority of the land in this section is farmland, shown unshaded in Fig. 1. The impact of the Snowy Scheme on this section of the basin is only on the channel of the Snowy River. There are no dams and no major water-using activities, other than recreational fishing where the main target species are introduced trout. It is here that the widely quoted claim that the flow of the Snowy has been reduced to only 1% of its natural level applies. Strictly speaking, this is true only for a 2 km stretch of the Snowy channel between the Jindabyne Dam and its junction with Cobbin Creek. The distribution of these flows through the year as a percentage of natural is shown in Figure 3. Natural flows are returned to the river by the tributaries, all of which are unregulated, for the remainder of the river's course.

Following public pressure on the issue, and consistent with the Governments' desires to corporatise the SMA, an agreement has been put in place to return 21% of natural flows to the Snowy at Jindabyne over the next 10 years, possibly rising to 28% later (Snowy Water Inquiry 1998; The State of New South Wales, The State of Victoria and the Commonwealth of Australia 2002). The cost to taxpayers of the restoration of 21% of flows will be $375 million over the ten year period. Figure 3 shows the flow pattern at Jindabyne, as a percentage of natural flow, when 28% of natural flow is returned to the river.

Just exactly what the benefit of this increased flow will be is the subject of some speculation (Finlayson, 1999). The original reduction in flow was very large and happened very quickly, yet the river took nearly 20 years to adjust (Tilleard 2001). Erskine et al.,

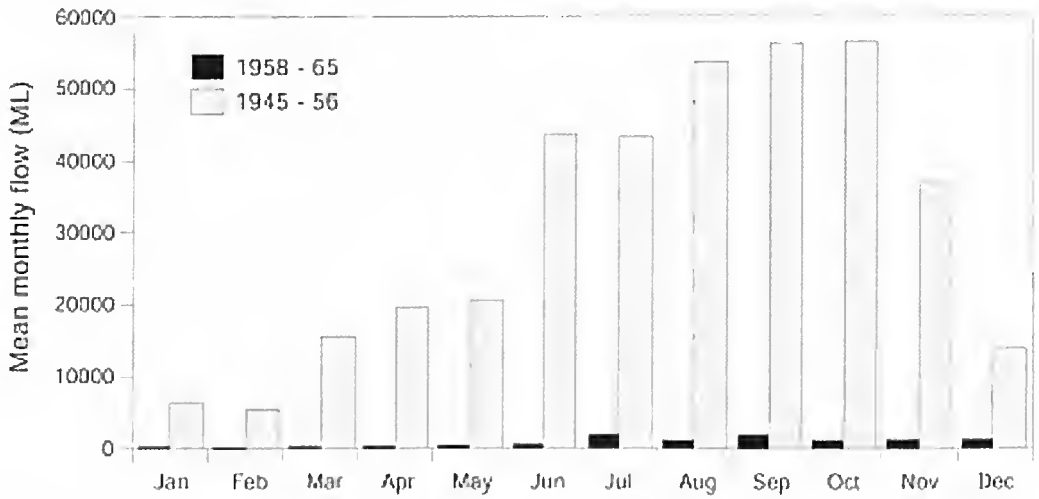


Fig. 2. Mean monthly flows for the Eucumbene River at Eastbourne. 1945-56 and 1958-65 are the periods of record pre and post the construction of the Eucumbene Dam respectively. (Data from Snowy Mountains Hydro-Electric Authority, 1970,1971.)

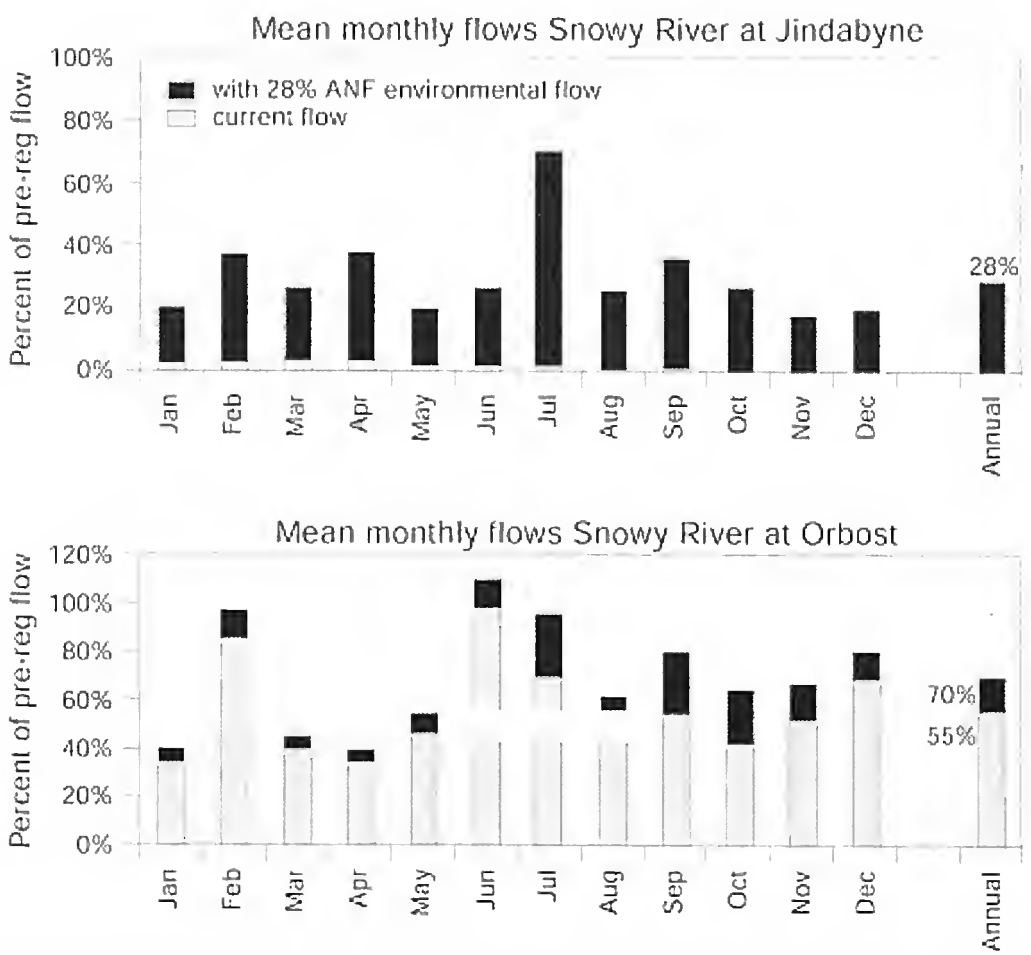


Fig. 3. Post-diversion flows and planned environmental augmentation of 28% for the Snowy River at Jindabyne and Orbost, expressed as percentages of the pre-diversion flows. (Source: Unpublished data, Dr Chris Gippel, Fluvial Systems Pty Ltd)

(1999) have described the impacts of this flow reduction on the channel. Just how the river will respond to the return of flows up to 21%, slowly over 10 years, is not known and probably depends more on the patterns of flows released than the total amount. For this amount of water to be released from Jindabyne, the outlet on the dam must be upgraded and the new outlet will incorporate a hydroelectric power plant (Snowy Hydro Limited, 2003). The pattern of water release is therefore likely to be determined by the commercial exigencies of power generation rather than the environmental needs for particular flow patterns.

Appropriate management of flows is not of itself sufficient to ensure that a river will be in good condition. Figure 4, a photo of the Snowy River at Dalgety in 1906, shows a river in poor condition irrespective of the flow it carries; riparian vegetation has been removed and stock access to the river is unrestricted. The site shown in Figure 4 was considered as a possible location for the federal capital, an option pushed strongly by the Dalgety Progress Committee (190-). It is interesting to speculate on the environmental trajectory of this section of the Snowy through the 20th century had the capital been located here.

As will be discussed later in relation to the lower Snowy floodplain section, there are many non-flow-related impacts that can degrade a river. Environmental restoration of the Snowy is not dependent solely on the return of some percentage of the natural flow.

The Escarpment

This is the largest of the 4 sections of the catchment and is deeply dissected by the rivers flowing across it (Fig. 1). The bulk of the area is forested and is held in State Forests and National Parks. The steep valley side slopes that in many cases directly abut the river channels indicate that this is geomorph-ologically the most active part of the catchment and the zone of highest sediment yield. The widespread preservation of the natural vegetation cover fortunately helps to minimise sediment yield. This section is sparsely populated and for much of its length here the Snowy River is difficult to access. There are no major water consuming activities and the river is used for fishing, whitewater rafting and canoeing.

The Floodplain

The fertile floodplain of the lower Snowy has been completely cleared of its native vegetation cover and drained for intensive agricultural use. The river as it crosses the floodplain is confined between natural levees that rise up to 4 metres above the surrounding floodplain. There are natural low points in the levees, referred to by fluvial geomorphologists as crevasses but known locally as gulches. Floodwaters leave the channel through these gulches to inundate the surrounding farmland. There is a long history in this area of building works to block off these gulches in an attempt to prevent the flooding of farmland.

The timing of impacts and responses on the lower Snowy River are shown in Figure 5. It can be seen there that the major impacts and the responses of the river occurred long before the construction of the Snowy Scheme and the resulting modification to the flows. Clearing and draining of the floodplain was largely completed before the end of the nineteenth century. The removal of snags (large woody debris) appears to have begun at least as early as 1880 and a team of men using a purpose-built barge with a steam

Fig. 4. The Snowy River at Dalgety in 1906. (Government Printing Office Collection, State Library of New South Wales, ML Ref. GPO 1/09873. Reproduced by permission of the Library Council of New South Wales.)

driven winch worked continuously on snag removal for at least 20 years in order to clear the channel for navigation (Finlayson & Bird 1989). The river's response to these activities was a period of channel widening around the turn of the nineteenth century. Snag removal from the river continued into the 1990s and ceased only when the functions of the Snowy River Improvement Trust were taken over by the East Gippsland Catchment Management Authority.

The farmers of the floodplain have agitated continually for works to mitigate floods and they supported the construction of the Snowy Scheme in the belief that it would help reduce the frequency and severity flooding on their farms. No rigorous analysis of this assumption was ever undertaken and the records show that while the scheme has reduced the size of minor floods, serious flooding of farmland has not been affected. Analysis of flow records for streams distributed across the Snowy catchment indicates that the major floods are generated by rainfall in the escarpment section and are therefore not affected by flow diversions at Jindabyne.

Associated with this concern over flooding has been the belief by local river managers that the channel of the lower Snowy has been infilled with sediment, the postulated source of which was agricultural soil erosion on the Monaro. Not only is there no evidence of infilling of the channel, and there are reliable channel cross section measurements dating back to 1920, it has been shown that most of the material eroded on agricultural lands in the Monaro has not yet been transported into the main channel of the Snowy River (Brizga & Finlayson 1991, 1994).

The planned return of flow to the Snowy River at Jindabyne will increase flows in the lower Snowy by 17% above their present levels but this is only 9% of the pre-regulation flow (Fig. 3). The impact in this section of the river will probably be slight but again will depend on the pattern of the releases. As described above, the serious environmental problems in this section of the river are not flow related. In recognition of this, the Bracks Labor Government in Victoria, following its election in 1999, allocated $30 million for non-flow related environmental restoration works on the lower Snowy. This is a significant allocation for such a short reach of a single river. The fact that the local electorate was held by an independent with the balance of power in the lower house was presumably a deciding factor.

Environmental restoration of the lower Snowy is to include the return of physical habitat to the featureless sand bed of this section of the river. This has clashed with local perceptions of the role of obstructions in the channel, such as snags, in exacerbating the flood problem, despite the plethora of expert opinion to the contrary. As a result, the planned restoration has become a locally contentious issue (Rule 2002).

This section of the river is the only part of the Snowy system where water is abstracted from the river for irrigation. The additional releases planned offer no benefit to irrigators as the agreement specifically precludes the use of this water for irrigation. How this provision will be policed is not known.

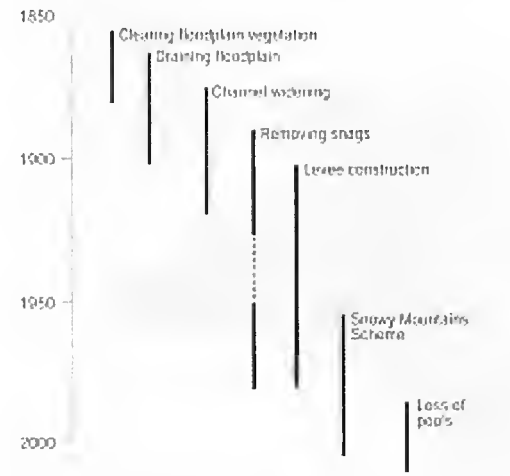


Fig. 5. Timing of impacts and responses on the lower Snowy River. (Source: Dr Mike Stewardson, School of Anthropology, Geography and Environmental Studies, The University of Melbourne)

DISCUSSION

The Victorian Government has set up processes by which funding is to be allocated to individual rivers for environmental restoration. The Victorian *Water Act* (1989) provides for the establishment of defined legal rights to water through the Bulk Entitlement Conversion and Streamflow Management Plan processes. Having defined these rights, it is then the government's intention to identify those rivers that are stressed due to inadequate flow regimes and to develop and implement comprehensive work plans to improve their condition (DNRE 1998). A second and more broadly based program is the development and application of the Index of Stream Condition (ISC, Ladson & White 1999).

The report of the scientific reference panel on stressed rivers identified 16 rivers across the State of

Victoria in the "very high" category of environmental stress (DNRE 1998). The Snowy River (in Victoria) is on this list but ranked at number 14. The Snowy was therefore not one of the 8 rivers identified for priority funding from the Rural Water Reform Package.

The first statewide survey of rivers using the ISC was carried out in 1999 and Figure 6 summarises the results for the major river basins of the state. The Snowy is one of only four basins with more than 51% of its stream length in excellent or good condition. There are 12 basins with less than 10% of stream length in good or excellent condition out of a total of 27 basins classified.

Despite the outcomes of these two scientifically based processes, the Victorian Government has allocated nearly $30 million to the environmental restoration of the lower Snowy, and this is in addition to the Victorian contribution to the $375 million to be spent increasing flow at Jindabyne to 21% of the pre-regulation total. This concentration of spending on a single river should be of concern to all those who wish to see a general improvement in the environmental condition of Victoria's rivers.

In the case of the Snowy River in Section 2, just downstream of the Jindabyne dam, the return of some additional flow to the river will not guarantee a significant improvement in river condition. There are many other issues which effect the environmental condition of a river, including the amount and distribution of habitat features such as large woody debris, catchment land use, the presence and abundance of introduced species, the pattern of variation in flow (floods/droughts/seasonal regime), water temperature, the nature and condition of the riparian corridor, and the presence of structures which prevent fish migration and the longitudinal movement of energy and nutrients. There is no evidence that all or any of these issues are to be addressed in the upstream sections of the Snowy. For example, the new outlet structure to be built on the Jindabyne Dam will not include a multi-level offtake tower to allow for flow released from the dam to match the natural seasonal temperature regime (Snowy Hydro Ltd 2003). There will therefore continue to be adverse impacts on native fish breeding patterns caused by unseasonally cold water released from the dam. This compounds the problem native fish already have in

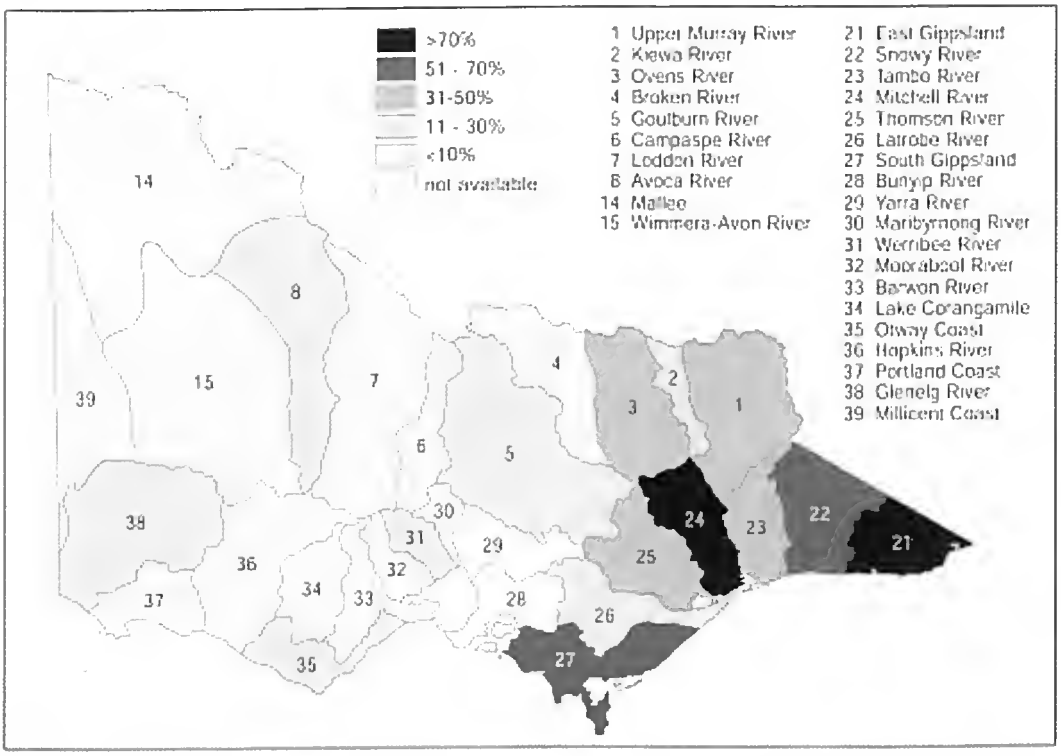


Fig. 6. Results of the 1999 survey of the Index of Stream Condition in Victoria. (Source: Victorian Water Resources Data Warehouse)

competing with introduced trout species in this section of the river. The debate has focussed on flow restoration, with little attention paid to these other issues.

There are two general points that can be made about the debate over the Snowy River. The first concerns the development of water policy in Victoria in particular and Australia more generally. There is no source of independent analysis of water policy in Australia. Politicians and an increasingly politicised bureaucracy develop policy on the run. As a result, politics, rather than good science, tends to dominate the development and implementation of policy. A complication to this situation is that the public servants who give policy advice in this area tend also to be those with managerial functions in the water area. Policy development is therefore compromised by this close connection to management.

The second point concerns the role of science. The absence of good science is everywhere evident in the Snowy debate and there is also resistance to scientists from local pressure groups if those scientists do not support the currently favoured position. Much of the scientific research on the Snowy has followed after, rather than led, the decision making process on the allocation of resources. Resources have been allocated on the basis of expediency, response to vocal pressure groups and political pork-barrelling while other rivers in the state continue to be degraded.

REFERENCES

Brizga S.O. & Finlayson B.L., 1991, *The Snowy River Sedimentation Study: Investigation into the distribution, transport and sources of sand in the Snowy River between Lake Jindabyne and Jarrahmond,* Department of Water Resources, Victoria. 72pp.

Brizga S.O. & Finlayson B.L., 1994, Interactions between upland catchment and lowland rivers: an applied Australian case study. *Geomorphology*, **9**: 189-201.

Byrne, G., 2000, *Schemes of Nation: a Planning History of the Snowy Mountains Scheme,* Unpublished PhD Thesis, Dept. of Art History and Theory, Faculty of Arts, University of Sydney.

Collis, B., 1990, *Snowy: The Making of Modern Australia*, Hodder and Stoughton, Sydney, 304pp.

Dalgety Progress Committee, 190-, *An Unique Site for the Federal City,* (Document held in the State Library of New South Wales, 90/1508)

DNRE, 1998, *Victorian Stressed Rivers Program, Priority Rivers for Restoration Plans: Findings of the Stressed Rivers Scientific Reference Panel*, Department of Natural Resources and Environment, Government of Victoria, East Melbourne, 15p

Erskine, W.D., Terrazzolo, N. & Warner, R.F., 1999. River rehabilitation from the hydrogeomorphic impacts of a large hydroelectric power project: Snowy River, Australia. *Regulated Rivers-Research & Management*, **15** (1-3): 3-24.

Finlayson B.L. & Bird J.F., 1989, *Initial Investigation into the Extent and Nature of the Current Sedimentation Problem on the Lower Snowy River*. Department of Water Resources, Victoria, 14pp.

Finlayson, B.L., 1999, The Snowy River Debate: the role of science in environmental activism, *Interaction*, **27**(2): 23-27.

Jennings, J.N. & Mabbutt, J.A., 1986. Physiographic outlines and regions, In *Australia—a Geography. The Natural Environment*, Vol. 1, D.N. Jeans, ed., Sydney University Press, Sydney. pp. 80–96.

Ladson, A.R. & White, L.J. 1999. *An Index of Stream Condition: Reference Manual*, 2nd ed., Department of Natural Resources and Environment, Government of Victoria, East Melbourne.

Rule, A., 2002, Alliance splits over plan to jam the Snowy, *The Age*, 16 June, 2002.

Snowy Hydro Limited, 2003. Jindabyne Dam – proposed outlet structure and auxiliary spillway, http://www.snowyhydro.com.au/images/jind_dam.jpg (accessed 30 March, 2004)

Snowy Mountains Hydro-Electric Authority, 1970. *Streamflow records of the Snowy Mountains region, Australia, to 1965*. Snowy Mountains Hydro-Electric Authority Cooma, N.S.W., (3 Vols).

Snowy Mountains Hydro-Electric Authority, 1971. *Streamflow records of the Snowy Mountains region, Australia, 1966 to 1970* . Snowy Mountains Hydro-Electric Authority Cooma, N.S.W., 279pp.

Snowy Water Inquiry, 1998. *Final Report.* Snowy Water Inquiry, Sydney.

The State of New South Wales, The State of Victoria & The Commonwealth of Australia,

Heads of Agreement: The Agreed Outcome of the Snowy Water Inquiry, 6 Deeember 2002.

TILLEARD, J.W., 2001. *River Channel Adjustment to Hydrologic Change*, Unpublished PhD Thesis, The University of Melbourne.

VANDERZEE, M. & TURNER, G., 2002. The Snowy flows again – intergovernmental eooperation on water reform, *Proceedings of the 4th Australasian Water Law and Policy Conference*, 24 & 25 Oetober 2002, Sydney.

PROCEEDINGS

OF THE

ROYAL SOCIETY OF VICTORIA

Volume 116

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE, VICTORIA 3000

© Copyright - Royal Society of Victoria Incorporated, 2004
ISSN 0035-9211

CONTENTS OF VOLUME 116

INTRODUCTION

KERSHAW A. P. & ORR, M. L. i
Environmental history of the Newer Voleanies of Victoria. Introduetion.

PROCEEDINGS

JOYCE, B. 1
The young Volcanic Provinee of Southeastern Australia: early study, physieal voleanology of the subprovinees, and eruption risk.

EDWARDS, J., CAYLEY, R. A. & JOYCE, E. B. 15
Geology and Geomorphology of Lady Julia Perey Island, a Late Mioecne submarine and subacrial voleano off the coast of Victoria, Australia.

SUTALO, F. & JOYCE, B. 37
Long basaltic lava flows of the Mt Rouse voleano in the Newer Volcanic Province of southeastern Australia

SUTHERLAND, F. L., GRAHAM, I. T. & ZWINGMANN, H. 51
Late Cenozoic basalts, Uplands Province, N.E. Vietoria: in relation to the Newer Volcanies basalts of Western Vietoria

SHERWOOD, J., OYSTON, B. & KERSHAW, A. P. 69
The age and contemporary environments of Tower Hill voleano, southwest Vietoria, Australia

SNIDERMAN, J. M. K., O'SULLIVAN, P. B., HOLLIS, J. D. & KERSHAW, A. P. 77
Late Pliocene vegetation and elimate ehange at Stoney Creek Basin, Western Uplands of Vietoria, Australia

KERSHAW, A. P., D'COSTA, D. M., TIBBY, J., WAGSTAFF, B. E. & HEIJNIS, H. 93
The last million years around Lake Keilambete, Western Victoria, Australia

HARLE, K. J., KERSHAW, A. P. & CLAYTON, E. 105
Patterns of vegetation change in southwest Vietoria (Australia) over the last two glacial/interglacial eycles: evidence from Lake Wangoom

KERSHAW, A. P., TIBBY, J., PENNY, D., YEZDANI, H., WALKLEY, R. & COOK, E. 139
Latest Pleistocene and Holocene vegetation and environmental history of the Western Plains of Vietoria, Australia

BUILTH, H. 163
Mt Eeeles lava flow and the Gunditjamara eonncetion: a landform for all seasons

Contents of Volume 116 continued overleaf

M. A. Treloar & L. J. B. Laurenson
Preliminary observations on the reproduction, growth and diet of *Urolophus cruciatus* (Lacepede) and *Urolphus expansus*, McCulloch (Urolophidae) in Southeastern Australia 183

S. G. Ryan, A. D. Miller & C. M. Austin
Allozyme variation and taxonomy of the river blackfish, *Gadopsis marmoratus* Richardson, in western Victoria 191

Ilse Bartsch & Janet Gwyther
A non-indigenous halacarid species in Victoria, southeastern Australia, *Isobactrus uniscutatus* (Rhombognathinae, Halacaridae, Acari) 201

Sandford, A. C.
A revision of *Lochkovella* Chlupáč, 1972 (Arthropoda: Trilobita) and a species from Lilydale and Tyers. Phacopidae of Victoria, Part 5 207

Denis J. Carr
Lejeuneaceae (Hepaticae) of Victoria; Additions and a restitution 221

Mark Thomas Warne
Description of *Loxocythere (Novoloxocythere) pelius* subgen. *et* sp. nov. (Ostracoda) from the Cenozoic of S.E. Australia with comments on species of *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 from Australian and Antarctic marine waters 233

Mark Thomas Warne
Observations on *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) (Ostracoda) from the Cenozoic of S.E. Australia with comments on species attributed to *Microcytherura* Müller, 1894 and *Hemiparvocythere* Hartmann, 1982 from Australian and New Zealand marine waters 243

Patricia L. Cook & Philip E. Bock
Exechonella (Exechonellidae: Bryozoa, Cheilostomata) from the Recent and Miocene of southern Australia 251

Patricia L. Cook & Philip E. Bock
Batopora and *Lacrimula* (Batoporidae) from Australia 269

TRANSACTIONS

P.N. Joubert OAM
Some Remarks on the 1998 Sydney-Hobart Race i

Finlayson, Brian L.
The Snowy River Debate xi

ROYAL SOCIETY OF VICTORIA

2004

Patron:	His Excellency, The Honorable John Landy, AC, MBE Governor of Victoria
President:	B. G. Livett, BSc(Hons), PhD
Vice-President:	P. G. THORN, BSc, PhD, DipPubPol
Immediate Past President:	N. W. Archibold, BA, MSc, PhD
Honorary Secretary:	J. W. Warren, MA, PhD
Honorary Treasurer:	B. J. W. McAULEY, BSc, MScp
Honorary Librarian:	D. A. McCann, PhD
Honorary Editor:	M. Grover, BEd, BSc(Hons)
Honorary Research Secretary:	P. G. Baines, BA(Hons), PhD

The above Office-bearers are *ex officio* members of the Council of the Society.

Other members of the Council are:

B. D. Birch, BSc(Hons), PhD
J. M. Bowler, AM, MSc, PhD, FAHA, FRSV
R. J. Foster, BE
H. Gardiner
M. R. Harris, BSc(Hons)
J. F. Lovering, MSc, PhD, FAA, FTS
P. C. Manins, BSc, BE(Hons), PhD, CCM, QEP, PSM, FTSE
N. F. Millis, AC, MBE, MAgrSc, PhD, FTSE, FRSV
L. Selwood, MSc, PhD
D.M. Stokes, BSc(Hons), PhD
M. Williams, BSc, MS

Executive Officer:
C. B. Van Megen

Honorary Financial Advisor:	Foster Streader Black Pty Ltd
Honorary Solicitors:	Phillips Fox
Honorary Auditor:	M. Kovassy, MAcc, CPA, AAIM
Trustees:	D. M. Churchill, BSc, MA, AAIM, PhD Professor J. W. Warren, MA, PhD Hon. Sir Edward Woodward, KT, OBE, LLM, QC

INSTRUCTIONS FOR AUTHORS

Papers considered for publication may be: Reviews, Reports of experimental or descriptive researeh, or Short Communications. Length of papers may vary but Short Communications should not exceed 1500 words. When an author submits a manuscript for consideration, it is assumed tbat it has never been published nor is under consideration for publication elsewhere.

SUBMISSION

The original and two copies of the typescript and all tables and figures should be submitted to the Executive Officer, Royal Society of Victoria, 9 Victoria Street, Melbourne, Victoria, 3000. Use International A4 bond paper, printed on one side only. In a letter of transmittal, give the names and addresses (postal and email) of tbe author or co-authors, also give the names, addresses and email addresses of three persons not directly associated with the work and outside the author's institution, who could act as referees. For all papers, presentation of the final manuscript on word-processed floppy disk is essential as well as a hard copy. Authors or their institutions may be requested to contribute towards the cost of publication of tbe paper and in the case of very long papers, such contribution is mandatory.

It will assist reviewers if related papers recently published or submitted elsewbere accompany the submitted manuscript.

FORMAT

All manuscripts should be written in clear and concise English. Use double spacing throughout; leave 30 mm margins around the text; number all pages. All measurements are to be expressed in SI units (eg μm, mm, m, km but not cm) and standard symbols and abbreviations used. Note, Ma refers to a date (eg 25Ma) not a time interval, which is written as 25 million years. When a number does not refer to a measurement it should be spelt out except when it is greater than nine. Wherever possible fractions should be written in the form x/y.

Geological papers must follow the Australian Code of Stratigraphic Nomenclature and should cite geological maps in the text with italics for the 1:63 360 series and full caps for the 1:250 000 series. New stratigraphic names should be registered with the Geoscience Australia (GA) Australian Stratigraphic Names Database. The GA website "How to define a litbostratigraphic unit" (http://www.ga.gov.au/minerals/strat_names/) is a useful guide.

The *Proceedings* uses Australian spelling according to the latest edition of the *Macquarie Dictionary* and where there is optional spelling for words we use the form used by Victorians traditionally. For example we use the following spelling; color, honorary, program.

Authors should follow the layout of beadings, tables and illustrations as presented in a recent issue of the *Proceedings*. Papers should be organised as follows:

1. *A brief title*, capitalised and, if possible, beginning with a key word.
2. *The name and address of the author(s)*, with numerical superscripts to distinguish addresses of multiple authors.
3. *A full reference to the paper*, leaving space for the printer's additions.
4. *A short abstract* of not more than 200 words describing the results (rather than the contents) of the paper.
5. *Up to 5 key words.*
6. *The main text.* Capitalise the first word of the introductory paragraph; do not use the heading 'Introduction'. Within the text up to three grades of headings may be used, typed as follows:

GRADE ONE HEADING

Grade two heading

Grade three heading. Followed by running text on the same line.

Refer to the papers illustrations in the text as "Fig. 1A, B", "Figs 1, 2"or "Figs 1-4", and indicate in the margins where the illustrations should be placed. Cite references in the text as Archbold (1998), (Archbold et al 1998) or (Archbold 1998: 2, fig. 1); multiple citations should be arranged chronologically. All references cited in the text must be listed at the end of the paper. Footnotes in the main text are not allowed. Where there are multiple authors for a reference, "et al." is used, and is not italicised.

In taxonomic works, synonymies should be of the same format as the following examples, with a dash preceding authors' names except in the case of reference to the original description.

Eudendrium generalis Lendenberg 1885: 351, pl. 6. — Lendenberg 1887: 16.

Eudendrium generale. — Hartlaub 1905: 515. — Watson 1985: 196-200, figs 40-52.

non *Eudendrium generale.* — Watson 1982: 89, pl. 10, fig. 3.

Eudendrium lendenfeldi Briggs 1922: 150. — Rosler 1978: 104, 120, pl. 20, figs 1-3.

Note that plate and figure numbers, etc. originally given in Roman numerals should be transliterated into Arabic figures; this is also the case in the main text and in the references.

7. *Acknowledgements.* The source of finacial grants and other funding, as well as the contribution of colleagues or institutions, should be aeknowledged. These should follow the main text and be as brief as possible.

8. *References.* These should conform in arrangement to the examples below. Journal titles must be cited in full as they appear on the title page.

Curtis, N.P., 2001. Germination of *Xanthorrhoea australis* using treatments that mimic post-fire and unburnt conditions. *Proceedings of the Royal Society of Victoria* 113(2): 237-245.

Bergson, H., 1928. *Creative Evolution.* MacMillan and Co.,

Ltd., London, xv+425 pp.

Rosen, B.R. & Turnesk, D., 1989. Extinction patterns and biogeography of scleractinian corals across the Cretaceous/Tertiary boundary. In *Proceedings of the Fifth International Symposium on Fossil Cnidaria including Archaeocyatha and Spongiomorphs*, P.A. Jell & J.W. Pickett, eds, Association of Australasian Palaeontologists, Brisbane, Queensland, 355-370.

Any other type, check previous recent copies of the *Proceedings*.

Personal communications and unpublished data are not to be listed in the reference list but should be mentioned in full in the text (eg P. Brown pers. comm. 2002).

9. *Tables and Figures*. Each table with its title should be typed on a seperate sheet. A separate sheet should also be used to list captions to figures in numerical order.

ILLUSTRATIONS

These must be designed for one or two column width (67 mm or 140 mm); maximum length is 193 mm. Composite Figures should be lablelled A, B, C, etc. (not a, b, c). Oversized illustrations, tables or maps may be accepted for publication as foldouts only if the author meets all costs involved in their production. Maximum size for foldouts is 193x285 mm.

Final submission of black and white figures electronically is encouraged as long as it is in a readily acceptable format (JPEG, TIFF, emf, wmf, pcx, pct, wpg, cdr). These can be supplied on 3.5" floppy disks, zip disks or CD (especially for figures with any grey shades) and accompanied by a high quality hard copy. Digital files must be supplied at a resolution of at least 600 d.p.i. at full size.

PROOFS

Authors will normally receive an 'Adobe Acrobat PDF' version of the mock page proofs; this is for the purpose of correcting printer's errors and not for altering the wording or substance of the paper. This should be returned, or comments emailed to the editor within 72 hours. If absent, authors should arrange for a colleague to check and return proofs to the editor on their behalf. Authors will be charged for excessive alterations at this stage.

REPRINTS

The corresponding author will be emailed an 'Adobe Acrobat PDF' of the final printed manuscript at the time of printing. Hardcopy reprints may be ordered by returning the order form that accompanies the mock page proofs.

Upon publication, copyright of the paper (including illustrations) is held by the Royal Society of Victoria. Any subsequent publication of any material shall be by written permission of the Society. Authors in Government institutions where copyright is retained by the Crown are exempt from transfer of copyright to the Society.

PROCEEDINGS OF THE
ROYAL SOCIETY OF VICTORIA

Volume 116, Numbers 1

CONTENTS

PROCEEDINGS

M. A. Treloar & L. J. B. Laurenson 183
Preliminary observations on the reproduction, growth and diet of *Urolophus cruciatus* (Lacepede) and *Urolophus expansus* McCulloch (Urolophidae) in Southeastern Australia

S. G. Ryan, A. D. Miller & G. M. Austin 191
Allozyme variation and taxonomy of the river blackfish *Gadopsis marmoratus* Richardson in western Victoria

Ilse Barusch & Janet Gwyther 201
A non-indigenous halacarid species in Victoria, southeastern Australia *Isobactrus uniscutatus* (Rhombognathinae: Halacaridae, Acari)

Sandford, A. C. 207
A revision of *Lochkorella* Chlupac, 1972 (Arthropoda: Trilobita) and a species from Lilydale and Tyers, Phacopidae of Victoria, Part 5

Denis J. Carr 221
Lejeuneaceae (Hepaticae) of Victoria, Additions and a restitution

Mark Thomas Warne 233
Description of *Loxocythere (Navolaxocythere) pelius* subgen. et sp. nov. (Ostracoda) from the Cenozoic of S.E. Australia with comments on species of *Antarctiloxoconcha* Hartmann, 1986 and *Loxoreticulatum* Benson, 1964 from Australian and Antarctic marine waters

Mark Thomas Warne 243
Observations on *Loxocythere (Loxocythere) ouyenensis* (Chapman, 1914) (Ostracoda) from the Cenozoic of S.E. Australia with comments on species attributed to *Microcytherura* Müller, 1894 and *Hemiparacythere* Hartmann, 1982 from Australian and New Zealand marine waters

Patricia L. Cook & Philip E. Bock 251
Exechonella (Exechonellidae: Bryozoa, Cheilostomata) from the Recent and Miocene Australia

Patricia L. Cook & Philip E. Bock 269
Batopora and *Lacrimula* (Batoporidae) from Australia

TRANSACTIONS

P.N. Joubert OAM i
Some Remarks on the 1998 Sydney-Hobart Race

Finlayson, Brian L. xi
The Snowy River Debate

© Royal Society of Victoria Incorporated, 2004